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THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 60 27 FEBRUARY 1991 NUMBER 1

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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

ANNALS OF CARNEGIE MUSEUM
VOL. 60, NUMBER 1, PP. 1-62 27 FEBRUARY 1991

SOUTH AMERICAN SPECIES OF *LOXANDRUS* LECONTE, 1852 (COLEOPTERA: CARABIDAE: PTEROSTICHINI)

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ABSTRACT

After consideration of the taxonomic position of *Loxandrus* LeConte among pterostichines, the South American species of the genus are divided, for convenience of identification, into 17 groups (not having taxonomic status). A key to the groups and keys to species of some groups are included. Fifty-five new species are described: *Loxandrus pseudomajor, L. latiusculus, L. adrimoides, L. amplithorax, L. planicollis, L. brunneicornis, L. rectibasis, L. longiusculus, L. orbicollis, L. marginepunctatus, L. punctatissimus, L. castanipes, L. punctimargo, L. cuyabanus, L. rotundicollis, L. rotundatus, L. marginalis, L. franiai, L. strigomeroides, L. mirei, L. depressibasis, L. subsinuatus, L. quadribasis, L. fulvus, L. iricolor, L. sericiventris, L. laetipes, L. affinis, L. profundestriatus, L. bonariensis, L. subquadratus, L. defanisi, L. sinuatus, L. simillimus, L. trapezicollis, L. macula, L. planoculis, L. davidsoni, L. kochalkai, L. kayae, L. photophilus, L. minasianus, L. latifascia, L. janeiranus, L. variabilis, L. humeralis, L. similis, L. cribratellus, L. pictoides, L. rubroniger, L. sinuatellus, L. ecuadoricus, L. brevis, L. reflexicollis, L. ornatellus.*

INTRODUCTION

In an earlier publication (Straneo, 1949), I described many new species of South American *Loxandrus*. Since then I have tried to secure as many specimens as possible of this genus because I was certain that many new species were still to be described. I have been able to publish (Straneo, 1951, 1953, 1958, 1967) several additional descriptions of new species. During my study of the genus *Argutoridius* Chaudoir, 1876 (Straneo, 1969*b*), I found that the type specimens of *Feronia* (*Argutor*) *apicalis* Waterhouse and *Feronia* (*Argutor*) *audouini* Waterhouse, which were included in the subgenus *Argutoridius* in the Coleopterorum Catalogus (Csiki, 1930), represent two species of *Loxandrus*.

I have examined abundant material of South American *Loxandrus* in the following collections: CMNH—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; UASM—Strickland Museum, University of Alberta, Edmonton, Alberta, Canada; MUB—Museum für Naturkunde, Humboldt University, Berlin; MLM—Miguel Lillo Museum, Tucumán, Argentina; CS—Collection Straneo, Viale Romagna No. 10, 20133 Milano, Italy. Holotypes and allotypes of some new species have been deposited in the collections of the United States National Museum of Natural History (USNM). Label data from type material have been transcribed verbatim. Where necessary, amplifications or translations of localities have been included in brackets.

These materials include a large number of well-defined new species. I intended originally to prepare a key to all species of South American *Loxandrus*. However, I consider that at present this is not possible because too many species remain undescribed.

In my key to genera and subgenera of South American Pterostichini (Straneo,

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Submitted 9 February 1990.

1977, 1979), I did not cite the views of Van Emden (1949) and Moore (1965) on the position of *Loxandrus* within the Pterostichini. According to them, the obliquely dilated protarsomeres and the absence of a scutellar striole are characters similar to those of the Old World subtribe Abacetina, which is distinguished by the short, broad, less excised mentum. Now, after publication of the monographs of North American and Mexican *Loxandrus* by Allen (1972) and Allen and Ball (1980), and after appearance of several other works on Carabidae (including, sometimes incidentally, *Loxandrus*) (Reichardt, 1977; Moore, 1979; Erwin and Sims, 1984), the reasons for keeping the *Loxandrus* series of genera in the Pterostichina are at least as numerous and as valid as those requiring their removal.

For example, a mentum shaped as in Abacetina is found in few species of *Loxandrus,* and is interspecifically variable. In many species of *Loxandrus,* the mentum is not short and is similar to the mentum of the Pterostichini *sensu stricto.* The scutellar striole is absent in some subgenera of *Pterostichus* (*sensu lato*) (*Trichopedius* Bedel, *Pedius* Motschulsky, etc.) and in some South American genera of Pterostichini *sensu stricto* (*Abaris* Dejean, *Eumara* Tschitschérine). In my opinion, the lack of a scutellar striole is only a specific character. An Australian genus of Pterostichina has obliquely dilated male protarsomeres similar to males of *Loxandrus.*

As for the type of chemical defense system reported for some Australian species of *Loxandrus* (Moore and Wallbank, 1968), which is different from that of some species of *Pterostichus,* I think that it is necessary to consider that the same chemical elements of defense also occur in Bembidiini and in some genera of Cicindelini and Carabini. As these groups are very far from *Loxandrus,* this identity of chemical defense systems is, in my opinion, no more than convergence of defense needs. This character may be very interesting for studies of insect ethology, but it is of uncertain or questionable taxonomic significance.

The larval characters could be of greater taxonomic significance. Arndt (1988) reported resemblance between the larva of *Abacetus villiersianus* Straneo and that of a species of *Loxandrus* (Bousquet, 1985). He also found that the larva of *A. villiersianus* has some characters in common with the larva of a *Pterostichus* (subgenus *Bothriopterus*). As the number of known larvae of species of *Loxandrus, Abacetus* and even *Pterostichus* is very small, I think that the question is wholly open and that it would be unwise to deduce any consequence from these few and conflicting affinities.

DEFINITIONS OF CHARACTERS

I have followed Tschitschérine (1898, 1900, 1901, 1903) in defining important characters of these insects in my previous descriptions, as also for the new species described in the present paper.

As in many other groups of Pterostichini, the chief characters for identifying *Loxandrus* species are found in the shape of the pronotum. Tschitschérine (1900) called attention to the anterior submarginal furrow which, at the anterior angles, continues without interruption from the inner line of the lateral border and runs along the anterior margin of the pronotum. This furrow delimits a border that I call the anterior submarginal border. Its shape may be employed to separate closely allied species. The variation in shape of this anterior submarginal border is schematically represented in Fig. 1. The border is limited (Fig. 1a) to a short trench near the anterior angles, or more or less extended (Fig. 1b) along the anterior margin. It is widely or briefly interrupted in the middle, or entire. It is narrow

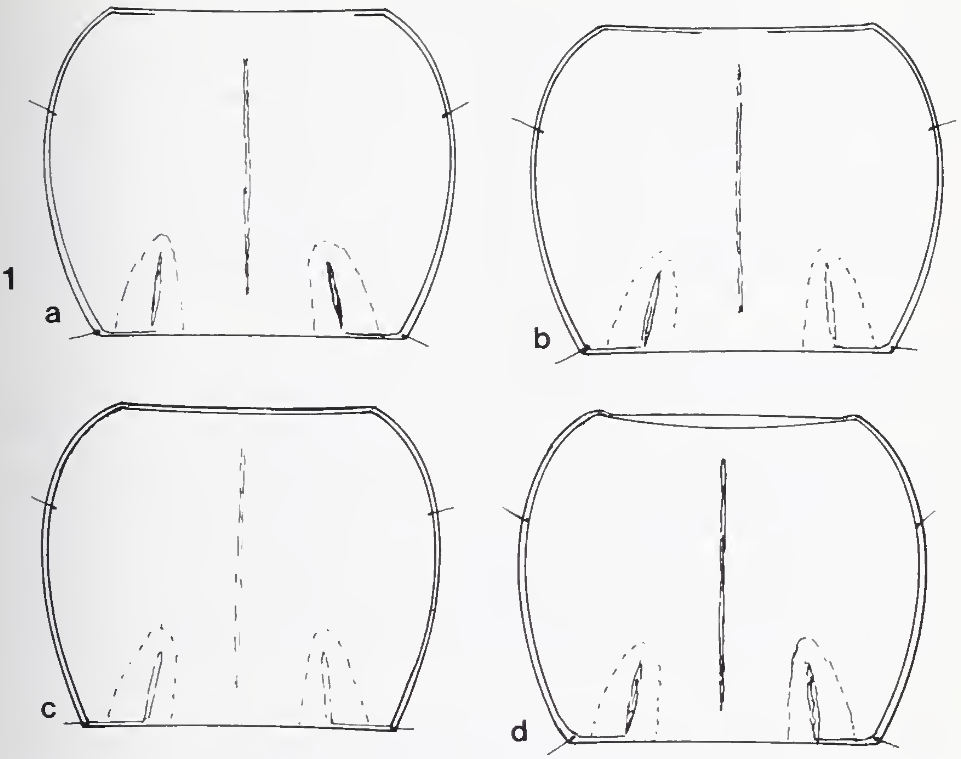

Fig. 1.—Schematic outlines of some characters of *Loxandrus*. Submarginal border of pronotum limited to anterior angles (a); more or less interrupted in middle (b); entire but narrow (c); entire, widened in middle (d).

throughout its length (Fig. 1c), or more or less widened in the middle (Fig. 1d). The shape of the anterior submarginal border is constant within species.

Another character, which has previously been given little importance, is the row of more or less coarse punctures (Fig. 2) present in some species along the basal part of the inner line of delimitation of the lateral border.

The metepisterna, which are strongly narrowed posteriorly in all species, have the outer sides generally longer than the anterior width. As suggested by Alluaud (1929), I indicate with r_d (*ratio dimensionum*) the ratio between the length and the maximum width of a specimen or of one of its parts. So the metepisterna in Fig. 3 have: Fig. 3a, $r_d = 1$; Fig. 3b, $r_d = 1.5$; Fig. 3c, $r_d = 2$.

The basal tarsomere (1) (and tarsomeres 2 and 3 in many taxa) of the hind tarsi is longitudinally sulcate on the exterior side, and the inner side is sulcate or not. If deeply sulcate, the upper surfaces of the bases of the tarsomeres are carinate (Fig. 4c) or not.

The apical tarsomere (5) of all tarsi, called the *onychium* by many authors, in many taxa has a few fine setae ventrally. This character, widely employed in the identification of Pterostichini and other tribes of Carabidae because it is easy to use for dividing groups of species, is of little use for *Loxandrus* species because these setae (as those of the lateral border of the pronotum) are caducous. I have observed in South American *Loxandrus* a few specimens in which all tarsi but

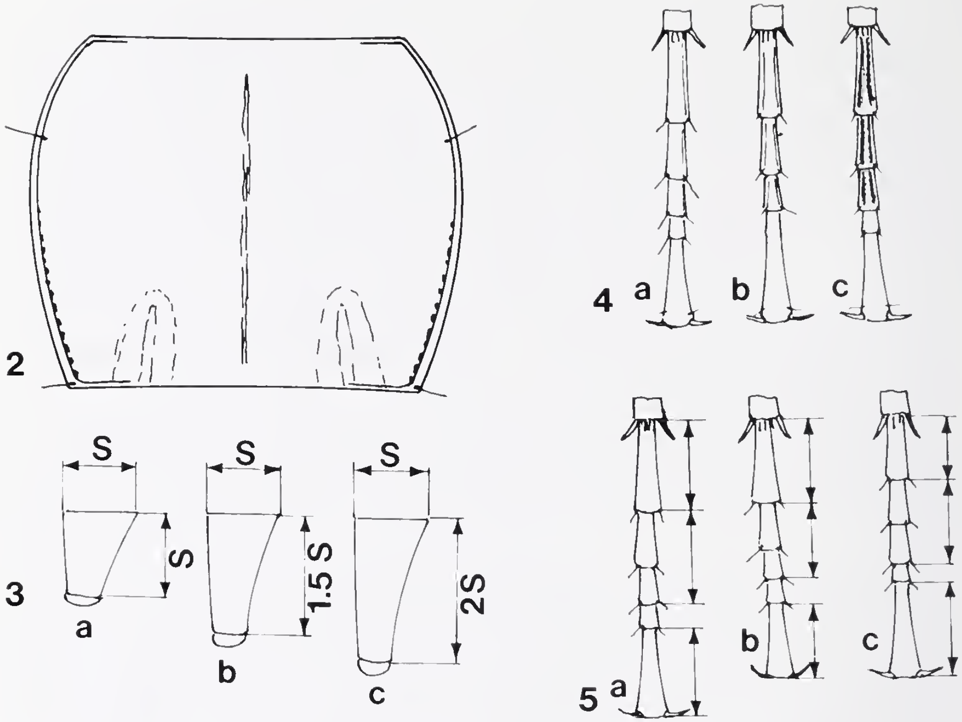

Fig. 2–5.—Schematic outlines of some characters of *Loxandrus*. 2. Pronotum with a row of punctures along basal part of lateral border. 3. Metepisterna: short, nearly as long as anterior width (a); length 1.5 times anterior width (b); twice as long as anterior width (c). 4. Hind tarsi: basal tarsomere with only external side sulcate (right side of figure) (a); both sides moderately sulcate (b); both sides markedly sulcate, dorsal surface carinate (c). 5. Reciprocal length of tarsomeres of hind tarsi: tarsomere 1 as long as tarsomere 5 and as long as 2 + 3 (a); tarsomere 1 longer than 5 and longer than 2 + 3 (b); tarsomere 1 shorter than 5 and shorter than 2 + 3 (c).

one were without setae ventrally. Before deciding whether a specimen belongs to a species with the apical tarsomere glabrous ventrally, it is necessary to examine carefully all the apical tarsomeres.

Finally, a useful character on the hind tarsi of *Loxandrus* mentioned by Tschitschérine (1900) is the relative length of the tarsomeres (Fig. 5): the basal tarsomere is longer (Fig. 5a), subequal to (Fig. 5b), or shorter (Fig. 5c) than the apical tarsomere or than the second and third tarsomeres together. Abdominal sternum VII is referred to in the text as "last sternum." It is the terminal one normally exposed.

Throughout this work I have used the word "stria." Some authors have adopted the recently coined word "interneur" (Erwin, 1974:4). I do not accept this word and hope for many reasons that it will not be adopted by other entomologists. The two most important reasons are, first, that I see no sense in replacing a word that until now was universally employed with perfect understanding and no inconvenience. Second, "stria" is a Latin word of international use, as is the great majority of words universally employed in entomological taxonomy. "Interneur" is a word recently invented without any logical or compelling reason. It is not an international word and could be at best employed only in English papers.

In most groups of Pterostichini the aedeagus is markedly sclerotized. Either the median lobe or parameres are interspecifically variable in shape in some taxa. The median lobe of many species has a well-developed apical blade which differs in shape between some species. Many closely similar species, separable only with difficulty on the basis of external characters, are distinguished by the shape of the apical blade. In South American *Loxandrus* species the aedeagus only rarely has a characteristic external shape. Generally, the median lobe is nearly or completely lacking an apical blade. The entire aedeagus is often so little sclerotized that its shape is very ill defined. Many species have very similar aedeagi with differences difficult to define. Therefore I give a sketch of the median lobe of the new species.

GROUPS OF SPECIES

To facilitate identification of the new species and to group closely allied species, I have arranged the South American *Loxandrus* species in 17 groups. These groups are only conveniences for identification of the species.

The characters used to define the groups are: 1) lateral part of basal margin of pronotum bordered or not bordered; 2) elytra with or without reddish or yellow-red spots or patterns; 3) elytra shiny (without microsculpture or with dense transverse lines not forming meshes) or sericeous (dull, microlines deeply engraved and meshed); 4) pronotum with sides rounded the entire length (or convergent straight to the base) or sinuate (or subsinuate) toward the base; 5) shape of the anterior submarginal border, entire or interrupted; 6) pronotal base punctate or entirely impunctate; 7) absence or presence, shape and arrangement of colored spots on elytra.

Key to Supraspecific Groups of Adult Loxandrus *from South America*

1. Base of pronotum bordered at sides, at least from basal impressions to hind angles; hind angles not markedly raised or reflexed 2
1′. Base of pronotum not bordered at sides; basal angles markedly reflexed (Fig. 66–68a) .... Group 17
2. Upper surface relatively shiny, not entirely sericeous 3
2′. Upper surface, at least elytra, entirely sericeous .... Group 16
3. Elytra without reddish or yellow spots or patterns; lateral border and apex of elytra not widely reddish or ferrugineous 4
3′. Elytra with some red or yellow spots or patterns or with apex widely reddish or ferrugineous 11
4. Pronotum with sides rounded, uniformly arcuate in some specimens, in others rounded on anterior half, thence convergent straight to base without sinuosity 5
4′. Pronotum with sides sinuate or subsinuate posteriorly 8
5. Base of pronotum impunctate (with or without one or two superficial punctures) 6
5′. Base of pronotum punctate (in some specimens punctures very few, and with row of punctures on inner line of lateral border) 7
6. Anterior submarginal border of pronotum entire, not interrupted in middle (Fig. 1c, d) .... Group 1
6′. Anterior submarginal border of pronotum widely interrupted in middle (Fig. 1a, b) .... Group 2

7. Anterior submarginal border of pronotum entire, not interrupted in middle (Fig. 1c, d) .... Group 3
7′. Anterior submarginal border of pronotum widely interrupted in middle (Fig. 1a, b), border narrow (Fig. 1a) or wide (Fig. 1b) .... Group 4
8. Base of pronotum impunctate 9
8′. Base of pronotum punctate (in some specimens punctures few, and with row of punctures on inner line of lateral border) 10
9. Anterior submarginal border of pronotum entire, not interrupted in middle (Fig. 1c, d) .... Group 5
9′. Anterior submarginal border of pronotum widely interrupted in middle, border in many specimens limited to near anterior angles (Fig. 1a, b) .... Group 6
10. Anterior submarginal border of pronotum entire, not interrupted in middle (Fig. 1c, d) .... Group 7
10′. Anterior submarginal border of pronotum widely interrupted in middle, border in many specimens limited to near anterior angles (Fig. 1a, b) .... Group 8
11. Elytra with only round, well-defined preapical sutural red spot (this spot in some specimens connected with apical margins of elytra by reddish apex of first interval) 12
11′. Elytra with pattern different 15
12. Base of pronotum impunctate 13
12′. Base of pronotum punctate 14
13. Anterior submarginal border of pronotum entire (Fig. 1c, d) .... Group 9
13′. Anterior submarginal border of pronotum interrupted in middle, border in many specimens limited to near anterior angles (Fig. 1a, b) .. Group 10
14. Anterior submarginal border of pronotum entire (Fig. 1c, d) ... Group 11
14′. Anterior submarginal border of pronotum interrupted in middle, border in many specimens limited to near anterior angles (Fig. 1a, b) .. Group 12
15. Elytra with humeral yellow or reddish band extended at least one third of elytral length, with or without other preapical spots .... Group 13
15′. Elytra without humeral band as above, or with short humeral spot, with or without other preapical spots 16
16. Each elytron with two small spots, one humeral and one preapical (not sutural, except in one species which has a preapical transverse narrow band) .... Group 14
16′. Elytra with pattern different .... Group 15

In the descriptions of the new species I do not reiterate the following characters common to all South American *Loxandrus*. All adults are winged and have two supraorbital setiferous pores and two setiferous pores on the lateral border of the pronotum. Each elytron has a pore at the base of the second stria and the umbilicate series of punctures is composed of a variable number of pores near the base, two or three spaced pores in the middle, and a preapical group of a few pores. The pore pattern is not constant within each species. The antennae of *Loxandrus* have antennomeres 1–3 glabrous (except normal tactile setae), and the protarsi of the males have tarsomeres 1–3 obliquely dilated.

The sketches of the pronotum that I present for each new species (and for a few species already described) illustrate shape and proportions. I present also sketches of the elytra for all species which have patterned elytra (Fig. 69–106).

Most of the sketches were drawn directly from specimens but a few were drawn from original descriptions. In the sketches some spots instead of being completely black are drawn in shading. This indicates that the whole spot is not clearly defined, or that its limits are not clearly defined, so that the spot seems diffuse or less vivid.

The descriptions of new species and observations about previously described species are presented by groups. For each group I list first the previously described species. Enclosed in parentheses after each species name is the length in millimeters, taken from the original descriptions.

GROUP 1

Characters of the group.—Elytra not sericeous, without red spots. Pronotum with base not punctate, bordered at sides; sides arcuate for entire length or convergent straight to base, not subsinuate; basal angles not raised; submarginal anterior border entire.

Described species.—*L. audouini* Waterhouse (8.4 mm); *L. laevicollis* Bates (10.5 mm); *L. integer* Tschitschérine (in the description length is omitted; as the author states that *integer* is very similar to *dubius* Curtis, the length is probably 10 mm); and *L. ruficornis* Tschitschérine (9 mm) (Fig. 9a, b).

Loxandrus pseudomajor, new species
(Fig. 6a, b)

Type specimens.—*Holotype,* male (CS): Uruguay, Artigas S. Gregorio, 28.XI.59, C. S. Carboneto. *Allotype,* female (CS), and *paratype,* male (CS): Uruguay (no further locality). Specimens examined: 3.

Diagnosis.—Group 1 species distinguished by large size, superficially very similar to *L. major* Straneo, from which it differs in having submarginal border not interrupted in middle. Moreover, pronotum of *L. pseudomajor* is shorter (r_d = 0.71; in *L. major,* r_d = 0.90). It appears to be closely allied to *L. audouini* Waterhouse, which is smaller (8.4 mm) with sides of pronotum more rounded.

Description.—Length 12 mm; greatest width 4.3 mm. Upper surface black, shiny; legs dark brown; antennae, tarsi and palpi completely ferrugineous red; underside brown. Head (including eyes) as long as wide (2.2 mm), moderately convex; temples no longer than quarter of eye; frontal impressions short, scarcely reaching level of antennal insertion; front between eyes moderately convex, smooth. Antennae elongate, extending beyond base of pronotum by two antennomeres.

Pronotum (Fig. 6a) anteriorly very convex, impunctate; anterior submarginal border entire, narrow; basal angles with vertex not blunt; basal impressions deep; space between impressions and basal angles convex; median longitudinal line thin, not deep; no anterior transverse impression. Microsculpture indistinct at 35×.

Elytra oblong, very convex, microsculpture very fine and dense, isodiametric; length 7 mm, greatest width 4.3 mm; basal border slightly curved toward very obtusely rounded humeri, obtusely joined to lateral border without angle; sides, behind posthumeral curve, very little arcuate, greatest width at $\frac{3}{5}$ length, thence rounded to apex; preapical sinuosity faint; striae deep, impunctate; intervals moderately convex; impressed puncture of interval 3 at midlength.

Underside entirely impunctate; prosternum partially sulcate longitudinally; metepisterna strongly narrowed posteriorly, 1.3 times longer than anterior width. Last abdominal sternum with 1 + 1 (male) and 2 + 2 (female) setae.

Legs slender; tarsomere 5 with few setae ventrally; tarsomeres 1–3 of hind tarsi grooved externally, not carinate; tarsomere 1 subequal in length to 5 and to 2 + 3.

Aedeagus with apical portion as in Fig. 6b.

Etymology.—The name proposed for this new species draws attention to its great resemblance to *L. major.*

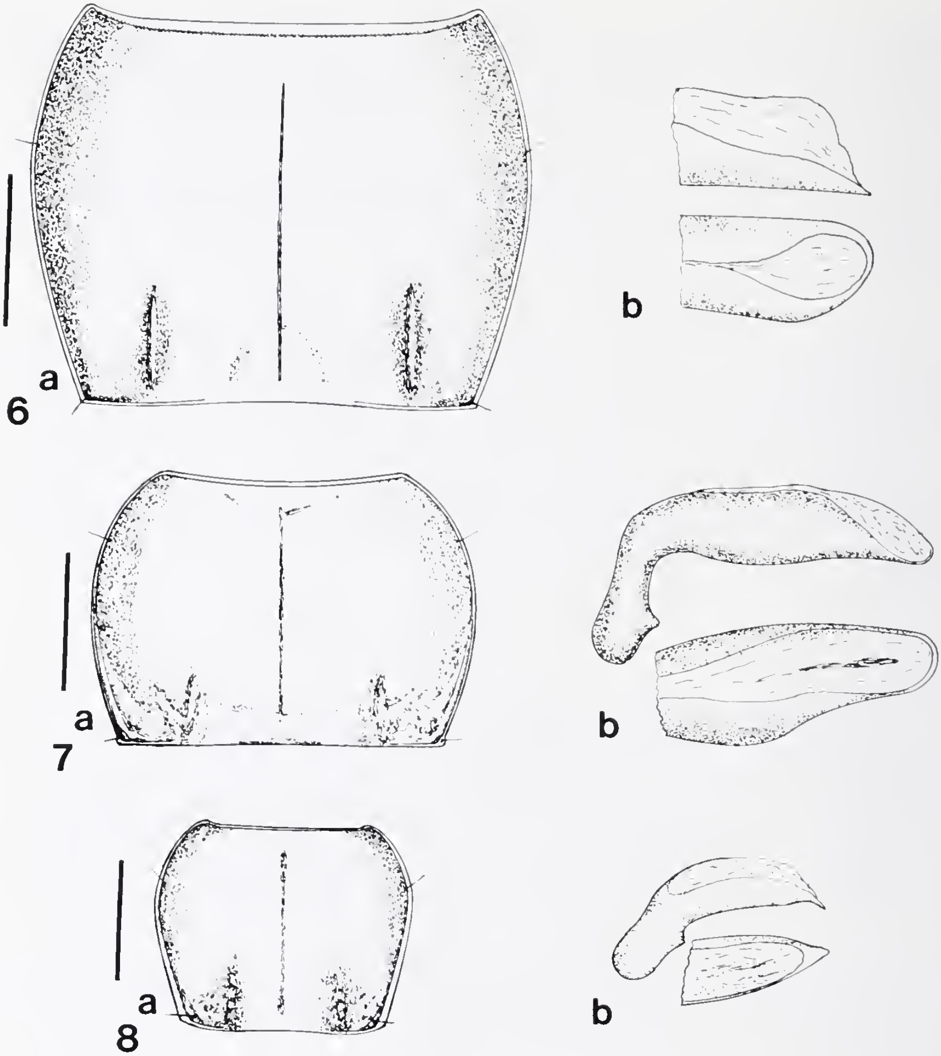

Fig. 6–8.—South American species of *Loxandrus*; pronotum (a) and median lobe of aedeagus (b). Scale line = 1 mm. 6. *L. pseudomajor*, new species. 7. *L. latiusculus*, new species. 8. *L. adrimoides*, new species.

Loxandrus latiusculus, new species
(Fig. 7a, b)

Type specimens.—Holotype, male (CMNH): Chapada, [Mato Grosso] Brazil, Acc. No. 2966. *Allotype,* female (CS) and 18 *paratypes* (CMNH, CS, UASM): same data as holotype. Specimens examined: 20.

Diagnosis.—Group 1 species similar to *L. laevicollis* Bates which also has tarsomere 5 of all tarsi glabrous ventrally, but which differs from *L. laevicollis* (according to the description) by more rounded sides of pronotum, obtuse and little dentate basal angles, entirely ferrugineous legs and antennae, and nearly smooth striae.

Description.—Length 9.2 mm; greatest width 3.5 mm. Upper surface piceous black, moderately shiny, not iridescent; legs, antennae, labrum and mandibles brown, more or less ferrugineous; underside brown blackish.

Head moderately elongate (2 mm × 1.65 mm); eyes moderately large, not very convex; temples long, less than ½ length of eyes and as convex as eyes; frontal impressions deep, reaching level of anterior supraorbital seta; front between eyes moderately convex, smooth. Antennae slender, extending beyond base of pronotum by three antennomeres.

Pronotum (Fig. 7a) moderately convex; disc widely and in many specimens irregularly flattened posteriorly; basal angles with trace of tooth; basal impressions deep, narrow, in some specimens accompanied by few irregular depressions; anterior transverse impression in most specimens well marked; median longitudinal line narrow, shortened at both extremities; microsculpture transverse, very fine and dense.

Elytra oblong, flattened, nearly 1.42 times longer than wide; microsculpture very fine and dense, isodiametric; basal border moderately curved toward slightly obtuse, very slightly rounded humeri and joined to lateral border at nearly 90°; sides uniformly and slightly curved, greatest width at ⅔ length; striae deep, nearly smooth; intervals moderately convex on disc, more so at apex; impressed puncture of interval 3 slightly before midlength.

Legs slender; tarsomere 5 of all tarsi glabrous ventrally; tarsomere 1 of hind tarsi slightly longer than 5 and subequal to 2 + 3.

Underside impunctate; abdominal sterna depressed at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 7b.

Loxandrus adrimoides, new species
(Fig. 8a, b)

Type specimens.—*Holotype,* male (CMNH): Brazil Alagoas, Sao Miguel dos Campos, IV.1984, F. Oliveira. *Allotype,* female (CS), and *paratypes,* 3 males, 2 females (CMNH, CS): same data as holotype. Specimens examined: 7.

Diagnosis.—Group 1 species distinguished by size, pronotal shape and proportions, and sharply pointed aedeagal apex.

Description.—Length 8.8 mm; greatest width 3.2 mm. Upper surface black, shiny, elytra more or less iridescent; femora, trochanters, palpi and antennomere 1 yellow; tibiae and tarsi slightly darker; antennomeres 2 and 3 markedly darkened toward apex, antennomeres 4–11 dark. Underside black, shiny, more or less iridescent; hind margin of sterna narrowly yellow-ferrugineous.

Head (including eyes) slightly longer (1.8 mm) than wide (1.5 mm); eyes large and very convex; temples as convex as eyes and about ¼ eye length; frontal impressions not very deep, very short, scarcely reaching level of antennal insertion; front between eyes convex with very fine and dense isodiametric microsculpture. Antennae thin and elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 8a) moderately convex; lateral border with row of small punctures; basal angles obtuse, not blunt, slightly raised; basal impressions deep with few very faint punctures or wrinkles at bottom; space between impressions impunctate; space between impressions and hind angles variable, from nearly flat to moderately convex, in some specimens with irregular small depressions or with 2 or 3 irregular punctures scattered from row of lateral border; median longitudinal line elongate and wide; microsculpture indistinct at 35×.

Elytra wide and subparallel, moderately convex; length 5.2 mm, greatest width 3.2 mm. Basal border slightly curved toward very obtusely rounded humeri and joined to lateral margin without angle; sides, behind pronounced posthumeral curve, nearly straight and slightly divergent to greatest width at ⅔ length, thence obtusely rounded to apex; striae deep, finely punctulate; intervals convex; impressed puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate, moderately elongate, with tarsomere 1 longer than 5 and shorter than 2 + 3.

Prosternum moderately sulcate longitudinally; proepisterna with some shallow punctures near coxae; metepisterna 1.5 times longer than wide, with many coarse punctures; angles of metasternum with many coarse punctures; abdominal sterna impunctate; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 8b.

Etymology.—The name proposed for this species comes from its great superficial resemblance to some species of the genus *Adrimus,* which is closely allied to *Loxandrus.*

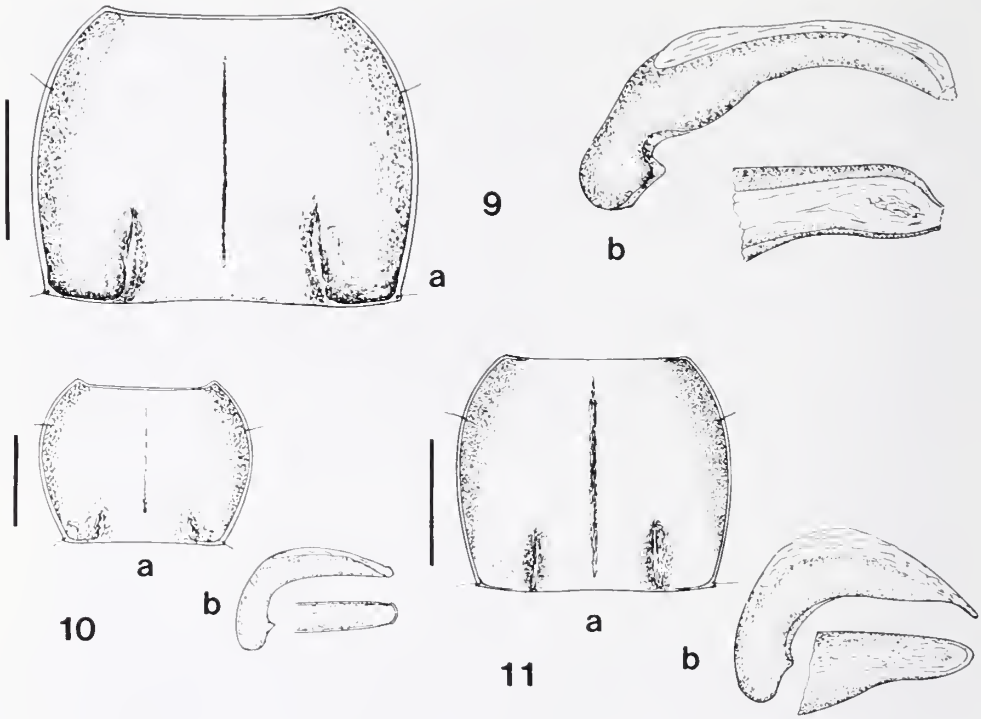

Fig. 9–11.—South American species of *Loxandrus*; pronotum (a) and median lobe of aedeagus (b). Scale line = 1 mm. 9. *L. ruficornis* Tschitschérine. 10. *L. amplithorax*, new species. 11. *L. planicollis*, new species.

Loxandrus ruficornis Tschitschérine
(Fig. 9a, b)

Among undetermined material of MUB are two specimens, male and female, of *Loxandrus* labelled "Brasilien, Cuyaba, O. Staudinger." They agree in every respect with the description of *L. ruficornis* Tschitschérine from the same locality and collector. I present sketches of the pronotum (Fig. 9a) and of the median lobe of the aedeagus (Fig. 9b), which is characteristic of the species. The apex of the median lobe is broken.

Loxandrus amplithorax, new species
(Fig. 10a, b)

Type specimens.—Holotype, male (USNM): Ecuador Napo km 24 n. Cotundo: Tena-Baeza rd. leaf litter: ridge top: 1097–1219 m. 3.V.1982 H. E. Frania & F. A. H. Sperling collectors. *Allotype,* female (USNM): same data as holotype. *Paratypes*: 4 (CS, UASM): same data as holotype (one very immature); 2 (CS, UASM): same data as holotype, but labelled "fruitfall" instead of "leaf litter"; 1 (UASM): same data as holotype, but "for. floor" instead of "ridgetop"; 3 (UASM CS): Ecuador, Napo, Campana Cocha: Puerto Misahualli, leaf litter, small ridge: 335 m. Specimens examined: 12.

Diagnosis.—Group 1 species with following unique combination of characters: small size (5–7 mm); labrum ferrugineous; antennae elongate; pronotum with sides markedly rounded and only slightly narrower than elytra; basal angles very obtuse. The angular preapical cut in the aedeagus is similar to that in the Group 8 species *L. similis* and *L. sinuatus* described later in this paper.

Description.—Length 6.2 mm; greatest width 2.7 mm. Upper surface black, shiny; elytra moderately iridescent; antennae, labrum, mandibles and legs pale ferrugineous. Underside black-brownish, slightly iridescent.

Head (including eyes) nearly as long as wide (1.1 mm); eyes large, very convex; temples nearly absent; frontal impressions very short, rounded; front convex between eyes; microsculpture indistinct at 35×. Antennae very elongate, extending beyond pronotal base by four antennomeres.

Pronotum (Fig. 10a) nearly as wide as elytra (*unde nomen*), convex; basal angles moderately marked, with very small tooth; basal impressions deep and irregular; space between impressions impunctate (in few specimens, two or three very small punctures on inner side of impressions); space between impressions and hind angles with wide rounded depression; microsculpture indistinct at 35×.

Elytra subparallel, ovate; length 3.85 mm, greatest width 2.7 mm; microsculpture indistinct at 35×; basal border joined to lateral margin at angle at obtusely rounded humeri; sides slightly rounded, greatest width at midlength; preapical sinuosity faint; apex of each elytron abruptly rounded; striae deep, nearly impunctate; intervals convex; impressed puncture of interval 3 very small, at midlength.

Legs moderately elongate; hind tarsomeres elongate, tarsomeres carinate on upper surface; tarsomere 5 glabrous ventrally; tarsomere 1 of hind tarsi longer than 5, subequal to 2 + 3.

Proepisterna with some very superficial punctures; metepisterna 1.2 times longer than anterior width, with many coarse punctures; angles of metasternum and sides of first abdominal sternum with many coarse punctures.

Aedeagus of characteristic shape (Fig. 10b), median lobe with very small angular cut on right side before apex.

GROUP 2

Characters of the group.—Elytra not sericeous, without red spots. Pronotum with basal angles not raised; sides arcuate for entire length or convergent straight to base, which is bordered at sides and impunctate; supramarginal border entire.

Described species.—*L. assimilis* Dejean (12.8 mm); *L. bolivianus* Tschitschérine (8.7 mm); *L. calathoides* Bates (10 mm) (Fig. 14); *L. curtatus* Tschitschérine (8 mm); *L. major* Straneo (13.5 mm); *L. melas* Straneo (7.7 mm); *L. obscurus* Straneo (8.8 mm) (Fig. 13); *L. simplex* Dejean (11.2 mm); *L. subfuscus* Tschitschérine (? = *apicalis* Waterhouse) (8.5 mm); and *L. tucumanus* Dejean (9 mm).

Loxandrus planicollis, new species
(Fig. 11a, b)

Type specimens.—*Holotype,* male (CS): Rep[ublica]. Arg[entina]. Pronunciamiento XI.69, Prov. Entre Rios. *Allotype,* female (CS), and 2 *paratypes* (CMNH, UASM): same data as holotype; 1 *paratype* (CS): R[epublica]. A[rgentina]. Entre Rios, Parana Guazu 27.VI.52. Specimens examined: 5.

Diagnosis.—Group 2 species with elytra slightly convex, similar to *L. tucumanus* Dejean. The latter species differs in having pronotum very convex with well-marked anterior transverse impression and much more convex eyes.

Description.—Length 8.8 mm; greatest width 3.1 mm. Upper surface piceous black, moderately shiny; elytra with slight iridescence; antennae and legs ferrugineous brown, palpi paler, mandibles and labrum darker. Underside black, not shiny.

Head moderately longer (1.6 mm) than wide (1.5 mm, including eyes); eyes large and convex; temples very short and abruptly convergent on neck; frontal impressions deep and straight, moderately elongate, reaching level of first supraorbital seta; front convex and smooth; microsculpture isodiametric.

Pronotum (Fig. 11a) very slightly convex, chiefly toward base (*unde nomen*); basal angles minutely dentate; basal impressions moderately deep; space between impressions and hind angles irregularly depressed; basal border at sides thin and narrow, base apparently completely unbordered; median longitudinal impressed line very deep, wide, nearly reaching base; microsculpture indistinct at 35×.

Elytra elongate; length 5 mm, greatest width 3.1 mm; slightly convex; microsculpture indistinct at 35 ×; humeri moderately obtuse, with small tooth; basal border nearly straight, joined to lateral margin at nearly 90° angle; sides, after slight posthumeral curve, nearly straight and divergent to greatest width at ⅗ length, thence more markedly arcuate to apex; preapical sinuosity moderate; striae 1–5 deep and smooth, remaining striae shallower and not reaching base of elytra; inner intervals moderately convex, external ones less so; impressed puncture of interval 3 conspicuous and at midlength.

Legs slender; tarsomeres 5 with some long thin setae ventrally; hind tarsomeres carinate dorsally; tarsomere 1 same length as 5, slightly shorter than 2 + 3.

Proepisterna smooth; metepisterna, angles of metasternum, and sides of two basal sterna (II and III) with many coarse punctures; remaining sterna impunctate with faint irregular depressions on sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 11b.

Loxandrus brunneicornis, new species
(Fig. 12a, b)

Type specimens.—Holotype, male (MUB): Brasilien [Brazil], Sta. Catharina [State] Lages, Hochland, Fruhstorfer S. *Allotype,* female (CS), and 4 *paratypes* (MUB, CS): same data as holotype. Specimens examined: 6.

Diagnosis.—Group 2 species distinguished by small size and shape of pronotum and aedeagus. The pronotum is shaped like that of *L. audouini* Waterhouse from Buenos Aires, but *L. brunneicornis* is larger and has anterior submarginal border of pronotum entire.

Description.—Length 7.2 mm; greatest width 2.7 mm. Upper surface brown, dark, moderately shiny, pronotum more so; antennomeres 4–11 ferrugineous-brown, tarsomeres and antennomeres 1–3 paler. Underside brown.

Head stout, moderately elongate, width (including eyes) 1.6 mm; eyes large and convex; temples very short, nearly absent; frontal impressions very short, foveate; front between eyes convex, smooth; microsculpture isodiametric. Antennae moderately elongate, extending slightly beyond pronotal base.

Pronotum (Fig. 12a) convex chiefly at slightly dentate basal angles; base not depressed, narrowly bordered at sides; basal impressions deep; space between impressions and hind angles very convex; median longitudinal line short, shallow; microsculpture indistinct at 35 ×.

Elytra subparallel, moderately elongate, convex; length 4.1 mm, greatest width 2.7 mm; microsculpture isodiametric, very fine and dense; basal border slightly curved toward humeri, latter obtusely rounded and joined to lateral margin without angle; sides behind humeri slightly curved, greatest width at ⅔ length; preapical sinuosity faint; apex abruptly rounded; striae deep, smooth, intervals very little convex; puncture of interval 3 slightly before midlength.

Legs with tarsomeres 5 with few thin setae ventrally; hind tarsomeres not sulcate on external side; tarsomere 1 nearly as long as 5 and slightly shorter than 2 + 3.

Underside entirely impunctate; metepisterna nearly twice as long as wide; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 12b.

Loxandrus calathoides Bates and
Loxandrus obscurus Straneo
(Fig. 14a, b, 13a, b)

I present sketches of the pronotum (Fig. 14a) and median lobe of the aedeagus (Fig. 14b) of *L. calathoides* Bates and *L. obscurus* Straneo (Fig. 13a, b). The shape of the aedeagus of *L. calathoides* is superficially similar to that of *L. ruficornis* Tschitschérine (Fig. 9b) of Group 1. The aedeagus of *L. obscurus* has its base very little sclerotized; it is unusually short and stout.

GROUP 3

Characters of the group.—Elytra without red patterns or spots, not sericeous. Pronotum with base bordered, punctate; hind angles not markedly raised; sides

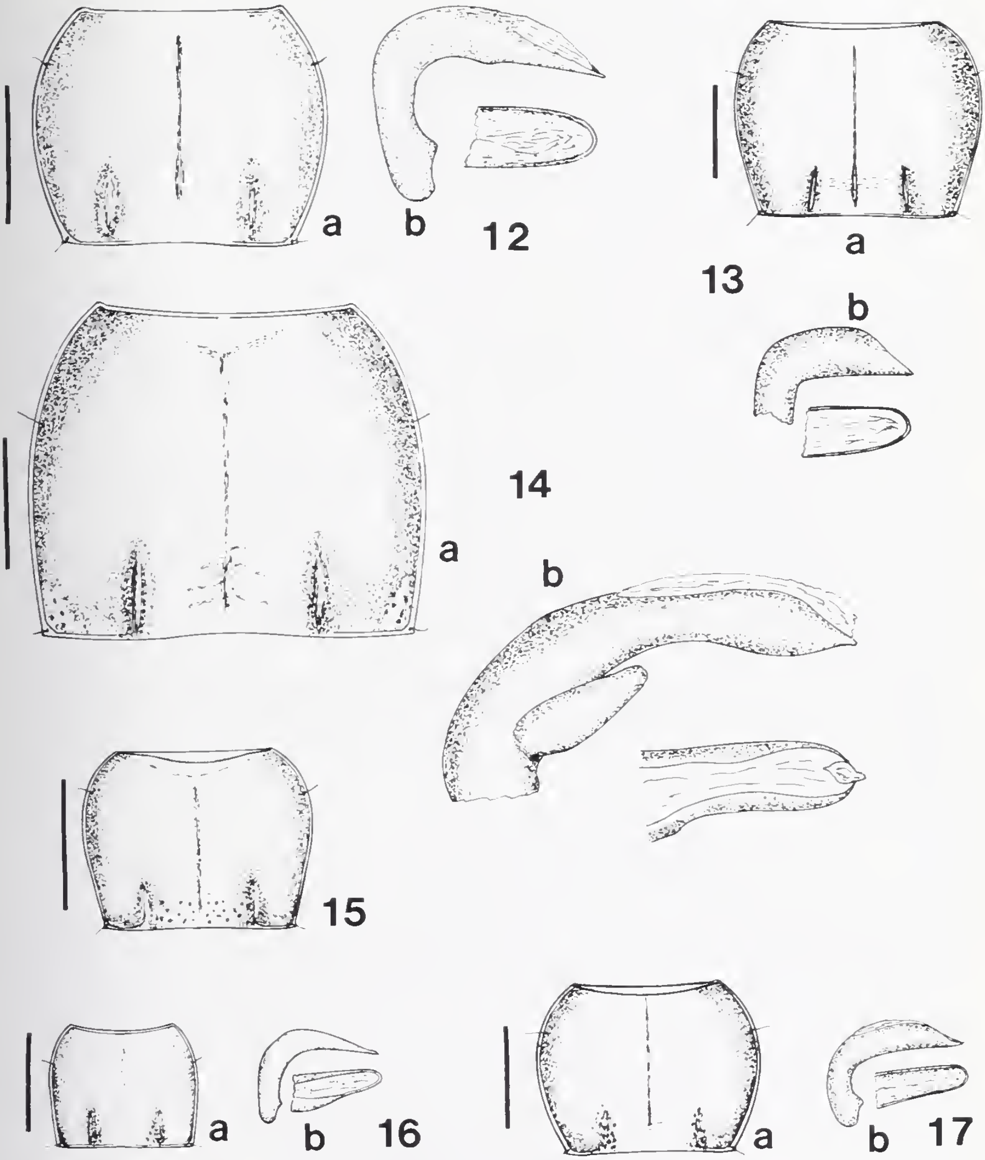

Fig. 12–17.—South American species of *Loxandrus*. Scale line = 1 mm. 12–14.—Pronotum (a) and median lobe of aedeagus (b). 12. *L. brunneicornis*, new species. 13. *L. obscurus* Straneo. 14. *L. calathoides* Bates. 15. Pronotum of *L. rectibasis*, new species. 16, 17.—Pronotum (a) and median lobe of aedeagus (b). 16. *L. longiusculus*, new species. 17. *L. orbicollis*, new species.

rounded or convergent straight to base, not subsinuate; anterior submarginal border entire.

Described species.—L. catharinae Tschitschérine (9.5 mm); *L. fulvicornis* Bates (10 mm); *L. sulcatus* Bates (12.3 mm); and *L. xanthopus* Bates (11 mm). *Loxandrus subparallelus* Bates (11 mm) probably belongs to this group, but Bates (1871) did not indicate whether sides of pronotum are straight or sinuate.

Loxandrus rectibasis, new species
(Fig. 15)

Type specimen.—*Holotype,* female (CS): Bolivia, Sta Cruz, Muflo de Chavez Ascension, 500 m, XI-63. Specimens examined: 1.

Diagnosis.—Group 3 species of small size (similar only to *L. longiusculus*), with pronotum of unique, subrectangular shape and anterior submarginal border dilated in middle. Shape of sides of pronotum is practically intermediate between species of Group 3 and Group 7.

Description.—Length 5.4 mm; greatest width 2.1 mm. Head and pronotum dark brown, shiny; elytra piceous black, shiny, slightly iridescent, with apical parts of lateral border ferrugineous red; legs and antennomeres 4–11 ferrugineous; palpi, tarsomeres and antennomeres 1–3 paler; labrum and clypeus reddish. Underside brown.

Head stout, nearly as long (1.3 mm) as wide (including eyes), eyes convex and moderately large; temples convex as eyes, not longer than ¼ eye length; frontal impressions wide, deep, reaching level of anterior border of eyes; front between eyes very convex, smooth, very shiny. Antennae elongate, extending beyond pronotal base by two antennomeres.

Pronotum subrectangular (Fig. 15), convex chiefly at anterior angles; anterior submarginal border widened in middle; base straight (*unde nomen*); basal impressions wide and deep; space between impressions and hind angles smooth and very convex; median longitudinal line deep and elongate; microsculpture indistinct at 35×.

Elytra subparallel-ovate; length 3.1 mm, greatest width 2.1 mm; basal border slightly curved toward obtusely rounded humeri and joined to lateral margin without angle; sides, behind moderate posthumeral curve, straight and moderately divergent to greatest width at midlength; striae deep, finely punctulate on disc; intervals moderately convex on disc, more so toward apex; impressed puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomere 1 grooved externally and nearly as long as 2 + 3 (hind tarsomere 5 cannot be described as both are mutilated in only known specimen).

Underside impunctate; metepisterna less than 1.5 times longer than anterior width; last sternum with 2 + 2 (female) setae.

Male unknown.

Loxandrus longiusculus, new species
(Fig. 16a, b)

Type specimens.—*Holotype,* male (UASM): Brasil Amazonas, Rio Negro, Cucui, igapo for. Sept. 11, 1978, G. E. & K. E. Ball, Brasil Exp. 1978. *Allotype,* female (UASM): same data as holotype. *Paratypes*: 1 female (CS), same data as holotype; 2 specimens (UASM, CS): Brasil Amazonas, Rio Demiti ca 0°37′N 66°48′W, below "Midland Camp" Igapo for. Sept. 11, 1978, G. E. & K. E. Ball, Brazil Exp. 1978. Specimens examined: 5.

Diagnosis.—Group 3 species characterized by small size, subrectangular pronotum, with sides very slightly curved and sparsely punctate, and long parallel elytra.

Description.—Length 5.25 mm (5–6 mm); greatest width 2 mm. Upper surface black, markedly iridescent; pronotum and suture of elytra slightly brownish; clypeus, labrum and other mouth parts and legs pale ferrugineous. Underside brown.

Head moderate, nearly as long (1 mm) as wide (including eyes); eyes large and convex; temples very short; frontal impressions deep, barely reaching level of anterior border of eyes; front between eyes convex. Antennae thin, extending beyond pronotal base by three antennomeres.

Pronotum subrectangular (Fig. 16a); length 1.2 mm; base with very narrow border from angles to level of scutellum; impressions deep and wide with few coarse punctures on inner side; few small punctures basally on inner line of lateral border; median longitudinal line moderate; microsculpture indistinct at 35×.

Elytra elongate, parallel (*unde nomen*); length 3.2 mm, greatest width 2 mm; humeri obtuse, rounded, basal border joined to lateral margin at obtuse angle; sides, behind short posthumeral curve, parallel for ⅘ length, elytra seemingly very long; preapical sinuosity moderate; apex of elytra blunt, not pointed; striae deep, finely crenulate; intervals convex; impressed puncture of interval 3 at about ⅗ length.

Legs slender; tarsomeres 5 glabrous ventrally; hind tarsomeres 1 and 2 slightly grooved on external side only; tarsomere 1 subequal to 5 and to 2 + 3.

Proepisterna shiny, impunctate; metepisterna 1.5 times longer than anterior width, more or less coarsely punctate, as also angles of metasternum and sides of first abdominal sternum; last abdominal sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus (Fig. 16b) wide in dorsal view and obviously narrowed short distance from apex.

Loxandrus orbicollis, new species
(Fig. 17a, b)

Type specimens.—Holotype, male (USNM): Ecuador Campana Cocha: e. Puerto Misahualli: leaf litter small ridge, 335 m, June 2, 1982. Ecuador Exp. 1982 H. E. Frania coll. *Allotype,* female (CS): same data as holotype. Specimens examined: 2.

Diagnosis.—Group 3 species characterized by combination of convex pronotum, very obtuse hind angles, small size, and closely punctate striae.

Description.—Length 6.5 mm; greatest width 2.6 mm. Upper surface black, shiny, markedly iridescent; clypeus, labrum, palpi, antennae and legs pale ferrugineous; lateral border of pronotum reddish, apical border and apex of suture of elytra reddish.

Head as long as wide (1.1 mm, including eyes); eyes large, convex; temples very short; frontal impressions small and shallow, barely reaching level of antennal insertion; front convex with fine and dense isodiametric microsculpture. Antennae elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 17a) convex; sides markedly and evenly rounded (*unde nomen*); length 1.6 mm; basal impressions wide with few coarse punctures on inner side, bottom, and along base of lateral border; median impressed longitudinal line moderate; microsculpture indistinct at 35×.

Elytra oblong-ovate, moderately convex; length 4 mm, greatest width 2.6 mm; humeri very obtuse, apex blunt; basal border joined to lateral margin at obtuse angle; sides, behind posthumeral curve, nearly parallel for ⅔ length, from there rounded to apex; preapical sinuosity very shallow, nearly absent; apex of each elytron blunt, not pointed; striae deep, closely punctate; intervals convex; impressed puncture of interval 3 small, at midlength; microsculpture indistinct at 35×.

Legs moderately slender; holotype without hind tarsi, but in allotype these carinate dorsally; tarsomere 5 with few setae ventrally; hind tarsomere 1 subequal to 5 and shorter than 2 + 3.

Proepisterna smooth; metepisterna wide, not more than 1.2 times longer than anterior width, with few coarse punctures; metasternal angles with few coarse punctures; first two abdominal sterna with some punctures at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 17b.

Remarks.—Only two specimens of this species are known. The allotype differs from the holotype only by the reduced punctation of the inner side of the basal impressions of the pronotum.

Loxandrus marginepunctatus, new species
(Fig. 18)

Type specimens.—Holotype, female (USNM): Bolivia, Cochabamba, Villa Tunari, Inundation for. rotting flood debris, 430 m, May 3–10, 1979, H. Frania coll. *Paratypes,* females: 2 (UASM, CS): same data as holotype; 1 (UASM): same data as holotype, but *ex* fruitfall. Specimens examined: 4.

Diagnosis.—Group 3 species similar to *L. fulvicornis* Bates, from which it differs by having sides of pronotum markedly punctate, basal angles obtuse, not subrectangular, and striae of elytra impunctate. No other species in Group 3 has sides of pronotum so coarsely punctate.

Description.—Length 9 mm; greatest width 3.7 mm. Upper surface black, shiny; pronotum and elytra very iridescent, with lateral border reddish; labrum, palpi, antennae and legs pale ferrugineous. Underside blackish, very iridescent, last sternum reddish.

Head stout, wider (width including eyes 1.75 mm) than long (1.6 mm); frontal impressions deep, very short, barely reaching level of antennal insertions; front convex, with fine and dense microsculpture. Antennae moderately elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 18); lateral border moderately wide, with outer margin little thickened, covered with coarse punctures, latter extended to base; anterior transverse impression short, deep; longitudinal median line very deep, not narrow; space between impressions and hind angles moderately convex; microsculpture indistinct at 35×.

Elytra ovate, slightly convex on disc, more so at apex; length 5.1 mm, greatest width 3.7 mm at midlength; humeri obtusely rounded; basal border joined to lateral margin at obtuse angle; sides moderately arcuate; preapical sinuosity obsolete; striae deep, impunctate; intervals convex; impressed puncture of interval 3 slightly behind midlength.

Legs with tarsomeres 5 glabrous ventrally; hind tarsomeres with upper surface carinate; hind tarsomere 1 longer than 5 and subequal to 2 + 3.

Proepisterna iridescent, with few punctures; metepisterna nearly twice as long as anterior width, distinctly punctate; metasternal angles and sides of sterna distinctly punctate; last sternum with 2 + 2 (female) setae.

Male unknown.

Loxandrus punctatissimus, new species
(Fig. 19a, b)

Type specimens.—Holotype, male (UASM): Brasil Amazonas, Rio Demiti ca. 0°37′N 66°47′W below Highland camp, igapo for. Sept. 11, 1978, Brasil Exped. 1978, G. E. & K. E. Ball Coll. *Allotype,* female (UASM): same data as holotype. *Paratypes*: 12 (UASM, CS, CMNH): same data as holotype; 18 (UASM, CS): Brasil, Amazonas, Rio Demiti, ca. 0°49′N 66°52′W igapo for., Loc. 2, Sept. 12, 1978, Bras. Exped. 1978, G. E. & K. E. Ball Coll.; 7 (UASM, CS): Brasil Amazonas, Rio Demiti ca. 0°52′N 66°57′W, "La Laguna" igapo for. Sept. 13, 1978, Brasil Exp. 1978, G. E. & K. E. Ball Coll. Specimens examined: 39.

Diagnosis.—Group 3 species characterized by unique very dense punctation of base of pronotum, punctation extending also to sides. This character distinguishes *L. punctatissimus* from all other South American *Loxandrus.*

Description.—Length 11.7 mm (11–13.5 mm); greatest width 4.75 mm. Upper surface black, shiny, except duller anterior part of head with pronounced isodiametric microsculpture; antennae, palpi and legs brown, femora darker, tarsi paler. Underside black, shiny, slightly to moderately iridescent.

Head slightly longer (2.3 mm) than wide (including eyes); eyes large, convex, posteriorly enclosed in temples; latter not more than ¼ eye length; frontal impressions deep, reaching level of anterior border of eyes; front moderately convex. Antennae very thin and elongate, extending beyond pronotal base by four antennomeres.

Pronotum (Fig. 19a) convex chiefly anteriorly, less so posteriorly, hind angles square; hind angles slightly dentate and slightly raised; base extensively covered (*unde nomen*) with moderately coarse but very dense punctures; basal impressions very wide and deep; anterior transverse impression generally moderate; median longitudinal line moderate, deepened basally, with some very short and thin transverse wrinkles; surface of space between anterior submarginal border and anterior transverse impression smooth to superficially punctulate or rugose; microsculpture indistinct at 35×.

Elytra oblong-ovate, moderately convex; length 8.4 mm, greatest width 4.8 mm; microsculpture indistinct at 35×; humeri obtuse, moderately marked; basal border joined to lateral margin with obtuse curve; sides moderately arcuate, greatest width slightly beyond midlength; preapical sinuosity clearly marked; apex of each elytron rounded; striae deep, with very fine and dense, nearly indistinct crenulation; intervals convex; impressed puncture of interval 3 at midlength.

Legs slender; hind tarsomeres carinate dorsally; tarsomeres 5 glabrous ventrally; hind tarsomere 1 longer than 5, slightly longer than 2 + 3.

Underside shiny; proepisterna, metepisterna and angles of metasternum densely punctate; last sternum with 1 + 1 (male) or 2 + 2 (female) setae (some males, including holotype, with 2 + 2 setae).

Aedeagus as in Fig. 19b.

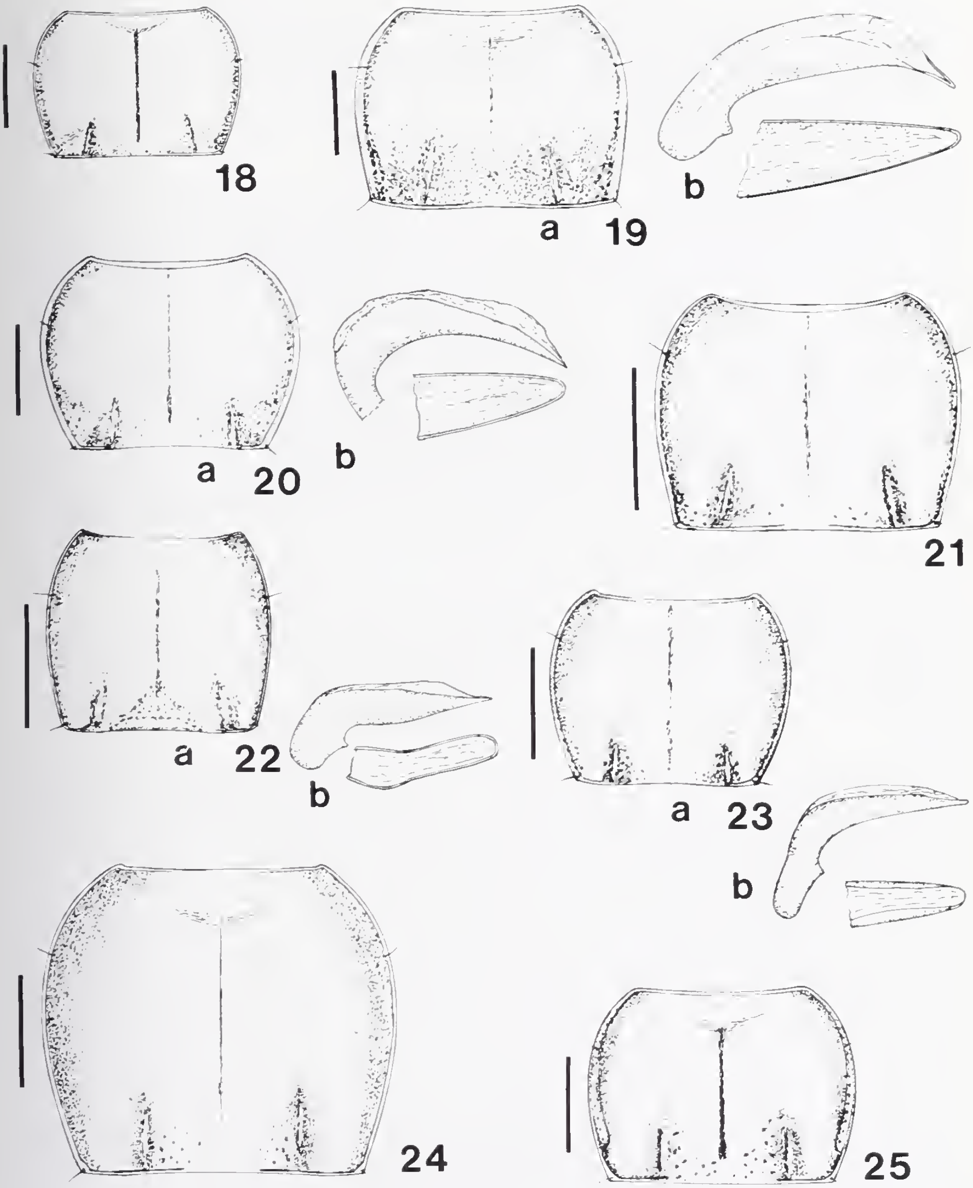

Fig. 18–25.—South American species of *Loxandrus*. Scale line = 1 mm. 18. Pronotum of *L. marginepunctatus*, new species. 19, 20.—Pronotum (a) and median lobe of aedeagus (b). 19. *L. punctatissimus*, new species. 20. *L. castanipes*, new species. 21. Pronotum of *L. punctimargo*, new species. 22, 23.—Pronotum (a) and median lobe of aedeagus (b). 22. *L. cuyabanus*, new species. 23. *L. rotundicollis*, new species. 24. Pronotum of *L. rotundatus*, new species. 25. Pronotum of *L. marginalis*, new species.

Loxandrus castanipes, new species
(Fig. 20a, b)

Type specimens.—Holotype, male (USNM): Ecuador Napo km 24 n. Cotundo, Tena-Baeza rd. seepage area nr. stream 1097–1219 m 4.V.1982. Ecuador exp.

1982 H. E. Frania & F. A. H. Sperling collectors. *Allotype,* female (USNM): same data as holotype. *Paratypes,* 4 males, 2 females (UASM, CS): same data as holotype. Specimens examined: 8.

Diagnosis.—Only species of Group 3 with pronotum markedly rounded at sides, base nearly smooth between impressions, and with some coarse punctures near basal angles and along base of lateral border.

Description.—Length 10.6 mm; greatest width 3.95 mm. Upper surface black, shiny, slightly iridescent; palpi, antennae and legs chestnut brown, femora darker. Underside black, shiny.

Head longer (2.15 mm) than wide (1.9 mm, including eyes); eyes large, moderately convex; temples short; frontal impressions moderately deep, very short, barely reaching level of antennal insertion; front smooth, convex, only moderately shiny, with very fine and dense microsculpture. Antennae moderately elongate, extending beyond pronotal base by one antennomere.

Pronotum (Fig. 20a); submarginal border moderately widened in middle; basal angles not dentate but well marked; basal impressions deep and wide; base with very few punctures between basal impressions and with some coarse punctures near angles and along basal part of lateral border; median longitudinal line deep, widened between basal impressions; microsculpture indistinct at 35×.

Elytra subparallel, moderately convex on disc, slightly more so posteriorly; length 6.3 mm, greatest width 3.95 mm; microsculpture indistinct at 35×; humeri slightly obtuse, moderately rounded; basal border joined to lateral margin at angle; sides slightly curved to greatest width at ⅔ length; preapical sinuosity moderate; apex of each elytron moderately rounded; striae very deep, nearly smooth; intervals convex; impressed puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres not sulcate on external side; hind tarsomere 1 as long as 5 and as 2 + 3.

Proepisterna with few punctures near coxae; metepisterna short, not more than 1.3 times longer than anterior width, very slightly punctate; metasternal angles and sides of first sternum very slightly punctate; remaining sterna depressed at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 20b.

***Loxandrus punctimargo*, new species**
(Fig. 21)

Type specimen.—*Holotype,* female (CS): Brasil Batatai [presumably Batatais, Sao Paulo State] X 1944 Pereira leg. Specimens examined: 1.

Diagnosis.—Group 3 species which resembles *L. calathoides* Bates (Fig. 14) in having pronotum moderately narrowed basally. However, *L. calathoides* has base of pronotum impunctate, sides less convergent to base, and anterior submarginal border interrupted in middle (Group 2). Of described species in Group 3, only *L. xanthopus* Bates approaches *L. punctimargo* in size, but latter species does not have pronotum much narrower than elytra and hind angles of pronotum not 90°, not protruded and not raised.

Description.—Length 8 mm; greatest width 3.1 mm. Upper surface piceous black, shiny, elytra markedly iridescent; labrum, palpi, antennae and legs pale ferrugineous. Underside black, moderately iridescent.

Head short, subtriangular, as wide with eyes as anterior margin of pronotum; eyes very large, convex, nearly hemispherical; frontal impressions very short, foveate, reaching level of antennal insertion; front between eyes convex, smooth; microsculpture fine and dense, isodiametric. Antennae moderately thin, extending beyond pronotal base by one antennomere.

Pronotum (Fig. 21); basal angles obtuse, not blunt; base nearly entirely narrowly bordered; basal impressions short and wide; few punctures either in middle or near basal angles and along basal part of lateral border; median longitudinal line wide, elongate; microsculpture indistinct at 35×.

Elytra convex, subparallel; length 5 mm, greatest width 3.1 mm; basal border moderately curved toward obtusely rounded humeri and joined to lateral margin at obtuse angle; sides, behind posthumeral curve, subparallel; greatest width at ⅔ length; preapical sinuosity moderate; striae deep, very finely punctulate; intervals moderately convex; impressed puncture of interval 3 slightly behind midlength.

Legs moderately slender; tarsomeres 5 with two very thin setae ventrally; hind tarsomeres with upper side carinate; hind tarsomere 1 longer than 5 and nearly as long as 2 + 3.

Proepisterna smooth; mesosternum with some moderate punctures; metepisterna nearly twice as long as anterior width, with many coarse punctures; metasternal angles with many coarse punctures; first two sterna punctulate and with wrinkles at sides, remaining sterna with depression on each side; last sternum with 2 + 2 (female) setae.

Male unknown.

GROUP 4

Characters of the group.—Elytra black or brown, without red patterns or spots, not sericeous. Pronotum with base bordered at sides; hind angles not raised; sides rounded or convergent straight to base, not subsinuate; base punctate; submarginal anterior border interrupted at middle.

Described species.—*L. curtatoides* Straneo (7.3 mm); *L. curtonotus* Bates (8.9 mm); *L. dubius* Curtis; *L. irideus* Straneo (10.4 mm); *L. macroderus* Bates (8.9 mm); *L. mattoanus* Tschitschérine (7 mm); *L. modicus* Tschitschérine (6.5–7.5 mm); *L. paraguayensis* Straneo (9.3 mm); *L. punctibasis* Straneo (8 mm); *L. rubescens* Bates (5.6–7.3 mm); *L. stenolophoides* Straneo (6.2 mm); *L. punctulatus* Straneo (9.7 mm; placed in this group although the submarginal border is barely interrupted in the middle); and *L. ripicola* Straneo (10.7 mm; base of the pronotum nearly impunctate).

Loxandrus cuyabanus, new species
(Fig. 22a, b)

Type specimens.—*Holotype,* male (MUB): Brasilien [Brazil: Mato Grosso State], Cuyaba, O. Staudinger. *Allotype,* female (CS): same data as holotype. *Paratype,* male (CS): Cuyaba, Matto Grosso (bought from Staudinger Bang Haas). Specimens examined: 3.

Diagnosis.—Group 4 species that is similar to *L. mattoanus* Tschitschérine, with which it agrees in many characters. Chief differences in new species are: smaller size, basal angles widely rounded; base of pronotum densely and markedly punctate; basal part of lateral pronotal border with row of punctures. *Loxandrus macroderus* Bates also has many characters in common with *L. cuyabanus,* but it is considerably larger.

Description.—Length 5.9 mm; greatest width 2.5 mm. Upper surface piceous black, shiny, with lateral border of pronotum, apical portion of elytral border and epipleura of elytra ferrugineous; elytra slightly iridescent; legs, palpi and antennomeres 1–3 pale yellow, antennomeres 4–11 brown. Underside piceous black, iridescent.

Head nearly as long as wide (1.25 mm); eyes very large and moderately convex; temples very short, nearly absent; frontal impressions short, barely reaching level of antennal insertion, shallow, narrow. Antennae thin, elongate, extending beyond pronotal base by nearly three antennomeres.

Pronotum (Fig. 22a) subrectangular, moderately convex; length 1.5 mm; basal angles moderately rounded; base slightly depressed in middle; basal impressions wide and deep, with external side very slightly inclined toward basal angles; space between impression and angles slightly convex, smooth; some faint punctures along lateral border; median longitudinal line deep anteriorly, less so posteriorly; microsculpture indistinct at 35 ×.

Elytra slightly convex, suboval; length 3.5 mm, greatest width 2.5 mm; microsculpture indistinct at 35 ×; basal border moderately arcuate toward slightly marked, blunt humeri, joined to lateral margin at nearly 90° angle; sides, behind short posthumeral curve, nearly straight and divergent to greatest width at $\frac{3}{5}$ length, from there uniformly rounded to apex; preapical sinuosity moderate; striae deep, markedly crenulate; intervals moderately convex; impressed puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 with two very thin setae ventrally; hind tarsomere 1 slightly longer than 5 and shorter than 2 + 3.

Underside impunctate; metepisterna 1.5 times longer than anterior width.

Aedeagus (Fig. 22b) immature and possibly deformed.

Loxandrus rotundicollis, new species
(Fig. 23a, b)

Type specimen.—*Holotype,* male (CS): Chanchamayo, Dpto Junin (Peru) 1200 m 13-X-61. Specimens examined: 1.

Diagnosis.—Group 4 species characterized by very rounded convex pronotum with slightly depressed space near hind angles and with row of punctures on basal half of lateral margin.

Description.—Length 6 mm; greatest width 2.35 mm. Upper surface black, shiny, not iridescent; legs, antennae and mouth parts pale ferrugineous. Underside black, shiny, iridescent.

Head moderately elongate, width (including eyes) 1.2 mm; eyes large and moderately convex; temples very short, nearly absent; frontal impressions moderately deep, short, extending on clypeus, barely reaching level of antennal insertion posteriorly; front between eyes convex, smooth; microsculpture isodiametric, microlines shallow. Antennae thin (incomplete in holotype).

Pronotum (Fig. 23a) very convex; length 1.5 mm; supramarginal border with short interruption in middle; base punctate only on inner declivity of short, deep and wide impressions; median longitudinal line very wide, nearly reaching anterior margin; microsculpture indistinct at 35×.

Elytra very convex; length 3.5 mm, greatest width 3.5 mm at midlength; basal border gently curved toward obtusely rounded humeri and joined to lateral margin at obtuse angle; sides, behind posthumeral curve, subparallel to greatest width, from there uniformly rounded to apex; preapical sinuosity moderate; striae deep, moderately punctate on disc; intervals convex; puncture of interval 3 very small, indistinct, at about midlength.

Legs slender; tarsomeres 5 with few setae ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 slightly longer than 5, slightly shorter than 2 + 3.

Underside with proepisterna smooth; metepisterna nearly 1.5 times as long as anterior width, with few coarse punctures; metasternal angles with few coarse punctures.

Aedeagus as in Fig. 23b.

Loxandrus rotundatus, new species
(Fig. 24)

Type specimen.—*Holotype,* female (CS): [Uruguay:] Montevideo. Specimens examined: 1.

Diagnosis.—Group 4 species characterized by large size and black coloration. The only other species of this group more than 10.0 mm in length are *L. ripicola* Straneo and *L. irideus* Straneo, both from Paraguay. *Loxandrus irideus* is a markedly iridescent species and *L. ripicola* is dark brown, shiny, with pronotal sides nearly straight toward base and basal angles dentate.

Description.—Length 11.8 mm; greatest width 4.4 mm. Upper surface black, relatively dull, chiefly elytra; legs, antennae and palpi dark brown. Underside dark, not shiny.

Head moderately longer (2.8 mm) than wide (2.2 mm, including eyes); eyes large and convex; temples short, continued to convexity of eyes; frontal impressions moderately deep, barely reaching level of anterior border of eyes; front between eyes convex and smooth; microsculpture isodiametric, very fine and dense. Antennae moderately elongate, antennomere 9 reaching base of pronotum (remainder missing in holotype).

Pronotum (Fig. 24) slightly convex at base, markedly convex anteriorly; sides markedly and uniformly rounded (*unde nomen*); length 2.7 mm; basal angles obtuse, not rounded; basal impressions oval, not divergent posteriorly, with some moderate punctures on inner sides; space between impressions and hind angles convex, smooth; median longitudinal line thin, shortened anteriorly and posteriorly; anterior transverse impression faint; microsculpture isodiametric, fine and dense.

Elytra elongate, oval; length 7.4 mm, greatest width 4.4 mm; convex on disc, more so toward apex; microsculpture isodiametric, microlines deep and dense; basal border narrow, slightly curved toward humeri and joined to lateral margin without angle; humeri obtusely rounded; sides, behind posthumeral curve, moderately arcuate to greatest width slightly behind midlength, from there rounded to apex; preapical sinuosity slight; striae deep, impunctate; intervals moderately convex on disc, more so toward apex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 with few setae ventrally; hind tarsomeres sulcate on both sides; hind tarsomere 1 nearly as long as 5 and as long as 2 + 3.

Underside impunctate, sericeous, with marked isodiametric microsculpture; metepisterna markedly narrowed posteriorly, nearly twice as long as anterior width; last sternum with 2 + 2 setae.

Male unknown.

Loxandrus marginalis, new species
(Fig. 25)

Type specimen.—Holotype, female (MUB): Brasilien [Brazil: Mato Grosso State] Cuyaba, O. Staudinger. Specimens examined: 1.

Diagnosis.—Group 4 species characterized by shape of pronotum and short elytra. I know no other *Loxandrus* with lateral border widened toward base, abruptly interrupted slightly before base, and with row of punctures laterally on pronotum.

Description.—Length 7.3 mm; greatest width 3.2 mm. Upper surface with head blackish brown, not shiny; labrum, mandibles, palpi and antennae pale ferrugineous; pronotum like head, but shiny, with lateral border and middle of base ferrugineous; elytra and legs entirely ferrugineous; epipleura and underside ferrugineous, with slight iridescence. (These colors may be due in part to immaturity.)

Head short, stout, width 1.5 mm with eyes; eyes large and convex; temples obsolete; frontal impressions deep, short, reaching only to level of antennal insertion; front between eyes smooth, convex, with marked isodiametric microsculpture. Antennae incomplete in holotype.

Pronotum (Fig. 25) characterized by unique lateral margin (*unde nomen*); length 1.7 mm; lateral border not narrow anteriorly, widened and deepened to ⁴⁄₅ length, then narrow and superficial; row of punctures extended entire length of lateral border; basal impressions moderately deep, sides very steep; space between impressions and hind angles impunctate, slightly convex, slightly depressed near hind angles; median longitudinal line narrow and deep; anterior transverse impression moderate; microsculpture near hind angles isodiametric.

Elytra moderately convex; length 4.3 mm, greatest width 3.2 mm; microsculpture marked, isodiametric; basal border markedly curved to humeri and joined to lateral border at obtuse angle; humeri obtuse and rounded; sides, behind posthumeral curve, nearly straight and parallel to greatest width slightly behind midlength; preapical sinuosity obsolete; striae deep, finely punctulate; lateral striae from 4 outward not reaching basal border; intervals moderately convex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 nearly as long as 5, shorter than 2 + 3.

Prosternum longitudinally grooved; proepisterna smooth; metepisterna slightly more than 1.5 times anterior width, with many coarse punctures; angles of metasternum and sides of first sternum with many coarse punctures; last sternum with 2 + 2 (female) setae.

Male unknown.

Loxandrus franiai, new species
(Fig. 26a, b)

Type specimens.—Holotype, male (USNM): Bolivia, Cochabamba, Villa Tunari, inundation for. rotting flood debris, 430 m, May 9–10, 1979, H. Frania coll. *Allotype,* female (USNM): same data as holotype. *Paratypes*: female (CS): same data as holotype; male (UASM): Bolivia, Cochabamba, between Corani and Villa Tunari, cloud for. leaf litter, 1820–1950 m, May 25–26, 1979, H. Frania coll. Specimens examined: 4.

Diagnosis.—Group 4 species characterized by the following unique combination of characters: color black, shiny; size 7 mm; pronotum with sides markedly rounded, lateral border with punctures on basal half; antennae very elongate; metepisterna short; hind tarsi short; median lobe of aedeagus with apex indented.

Description.—Length 7 mm (7–7.5 mm); greatest width 2.8 mm. Upper surface black, shiny, not or very slightly iridescent; mandibles reddish; antennae, palpi, legs, trochanters pale piceous brown. Underside blackish, slightly iridescent; apical margin of last sternum reddish.

Head stout, as long (1.3 mm) as wide (including eyes); eyes large and very convex; temples very short; frontal impressions deep, short, round; front between eyes moderately convex, with very fine

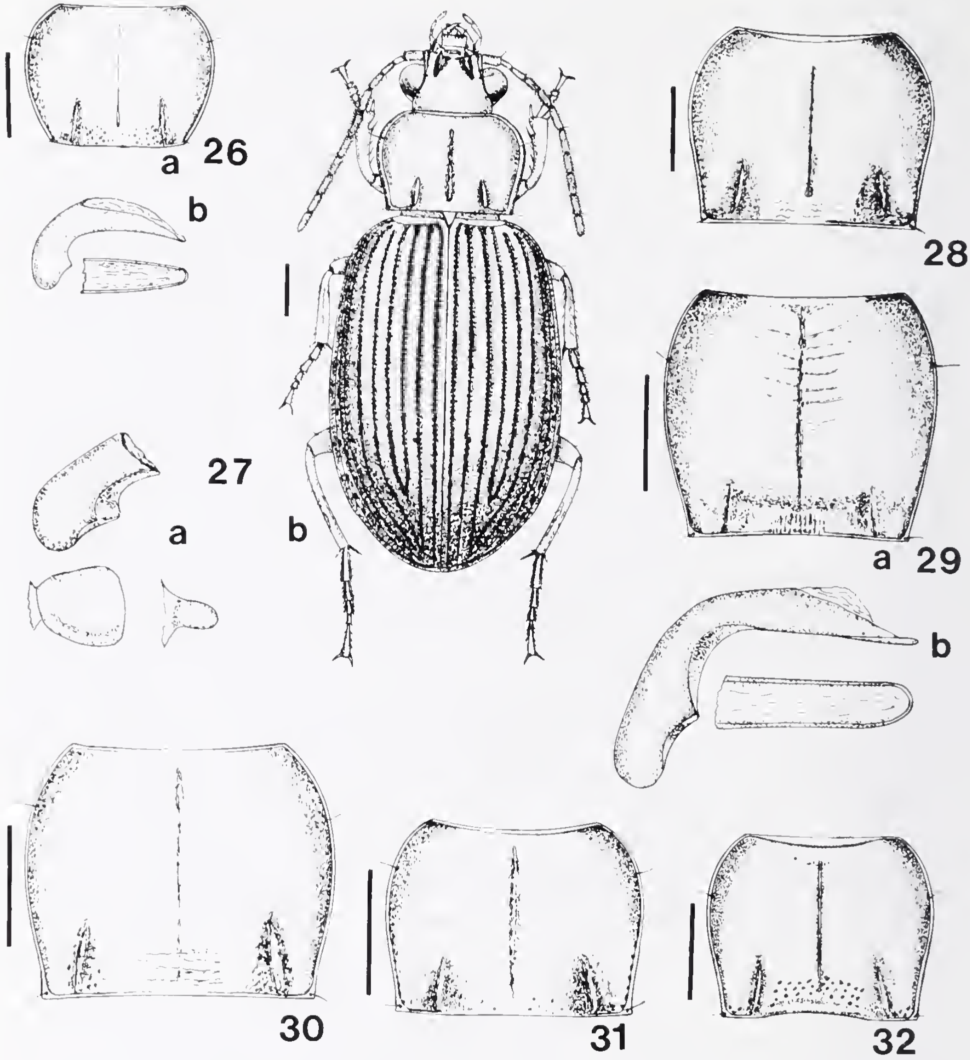

Fig. 26–32.—South American species of *Loxandrus*. Scale line = 1 mm. 26. Pronotum (a) and median lobe of aedeagus (b) of *L. franiai*, new species. 27. Habitus (a) and median lobe of aedeagus (b) of *L. strigomeroides*, new species. 28. Pronotum of *L. mirei*, new species. 29. Pronotum (a) and median lobe of aedeagus (b) of *L. depressibasis*, new species. 30–32.—Pronotum. 30. *L. subsinuatus*, new species. 31. *L. quadribasis*, new species. 32. *L. brullei* Waterhouse.

and dense microsculpture. Antennae very elongate, extending beyond pronotal base by four antennomeres.

Pronotum (Fig. 26a); basal part of lateral border with row of 7–12 punctures; basal impressions deep, moderately wide; base between impressions coarsely punctate; basal angles obtuse, blunt; median longitudinal line shallow, nearly linear; microsculpture indistinct at 35×.

Elytra oblong ovate, moderately convex on disc, more so toward apex; length 4 mm, greatest width 2.8 mm slightly past midlength; humeri obtuse, rounded; basal border joined to lateral margin without angle; sides nearly uniformly arcuate; preapical sinuosity moderate; apex of each elytron not blunt; striae very deep, markedly and densely punctate; intervals very convex; puncture of interval 3 very small and at midlength; microsculpture indistinct at 35×.

Legs moderately slender; hind tarsomeres with upper surface carinate; tarsomere 5 of each leg glabrous ventrally; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Underside shiny; proepisterna iridescent, smooth; metepisterna short, only 1.2 times as long as anterior width, with few coarse punctures; punctures more numerous on metasternal angles; sterna not punctate at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 26b. The apex is unique.

GROUP 5

Characters of the group.—Elytra black or brown, without red spots or patterns, not sericeous. Pronotum with base bordered at sides; hind angles not raised; sides sinuate or subsinuate toward impunctate base; anterior submarginal border entire.

Described species.—*L. egae* Straneo (10.4 mm); and *L. ater* Tschitschérine (11–12 mm; as the author states that the sides of pronotum toward base are "rectilignes (ou à peine appréciablement subsinués)," this species probably belongs to this group).

Loxandrus strigomeroides, new species

(Fig. 27a, b)

Type specimens.—*Holotype,* male (MUB): Serra Geral Urwald Dr. Heusel [green label]. *Allotype,* female (CS): same data as holotype. *Paratypes*: male, decidedly immature (CS): Porto Alegre Heusel; female (MUB): Guagua Venez. [not clear], and a second label: 2930, immature. Specimens examined: 4.

Diagnosis.—Group 5 species characterized by enormous eyes (Fig. 27c), pronotal shape with deep basal impressions, and deep punctulate striae.

Description.—Habitus as in Fig. 27a. Length 10.5 mm; greatest width 4.4 mm. Upper and ventral surface black, shiny; elytra iridescent; antennae brown; legs dark brown; tarsi and palpi ferrugineous red. (Two immature specimens completely brown.)

Head short and wide; eyes enormous, more than hemispherical; front between eyes convex, smooth. Antennae thin, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 27a); basal impressions deep, moderately wide; space between impressions and hind angles moderately convex; microsculpture indistinct at 35×.

Elytra moderately convex on disc, more so on apical declivity; microsculpture fine, scarcely distinguishable at 35×; preapical sinuosity obsolete; striae deep and distinctly punctulate; intervals convex; puncture of interval 3 at nearly ⅔ length, very small.

Legs moderately slender; tarsomeres 5 with some setae ventrally; hind tarsomeres markedly sulcate on exterior side, less so on interior side; hind tarsomere 1 nearly as long as 5 and nearly as long as 2 + 3.

Underside with proepisterna smooth, iridescent; mesosternum, metepisterna and angles of metasternum with some coarse punctures; metepisterna nearly 1.5 times as long as anterior width; sides of sterna depressed and punctulate.

Median lobe of aedeagus of holotype missing apical half, probably broken in life, with surface of fracture healed and black (Fig. 27b); parameres normal for *Loxandrus.*

Remarks.—This species is very unusual among *Loxandrus* known to me. It has an extraordinary resemblance to some species of the genus *Strigomerus* Chaudoir (African genus of the tribe Caelostomini), and so at first I thought it was mislabelled. But a study of the characters confirms that it is a *Loxandrus.* The name proposed for this species points out this resemblance.

Loxandrus mirei, new species

(Fig. 28)

Type specimen.—*Holotype,* female (CS): Bolivia Sta Cruz, Ichilo X.62, Buena Vista 400 m. Specimens examined: 1.

Diagnosis.—Group 5 species characterized by small size, shape of pronotum with impunctate base, and markedly and completely bordered prosternal process (a rare character in South American *Loxandrus*).

Description.—Length 7.3 mm; greatest width 2.9 mm. Upper surface piceous black, shiny, elytra iridescent; lateral margin of pronotum and elytra brown; legs, palpi, and antennomeres 1–3 pale ferrugineous, antennomeres 4–11 slightly darker; labrum and mandibles dark brown. Underside black, iridescent.

Head small, width (including eyes) nearly 1.2 mm; eyes moderately large and convex; temples nearly absent; frontal impressions small and short, barely reaching level of antennal insertions; front between eyes convex, smooth; microsculpture isodiametric, very fine and dense. Antennae slender, extending beyond pronotal base by two to three antennomeres.

Pronotum (Fig. 28) very convex near anterior angles; anterior submarginal border distinctly widened in middle; basal half of lateral border with row of very small punctures; base straight, narrowly bordered to level of scutellum; basal impressions deep, wide, shortened toward base; space between impressions and hind angles moderately convex; microsculpture indistinct at 35×.

Elytra oblong-ovate, moderately convex; length 4.5 mm, greatest width 2.9 mm; microsculpture indistinct at 35×; basal border slightly curved toward slightly obtuse and rounded humeri and joined to lateral margin at nearly 90° angle; sides, behind slight posthumeral curve, nearly straight and divergent to greatest width at about ⅔ length, thence gradually convergent to moderately obtuse apex; striae deep, nearly smooth; intervals moderately convex; puncture of interval 3 slightly behind mid-length.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Prosternal process markedly and completely bordered; proepisterna and mesosternum impunctate; angles of metasternum with many punctures; metepisterna nearly 2.0 times as long as anterior width, with few small punctures; first two sterna rugoso-punctate, remainder with irregular depressions on sides.

Male unknown.

Etymology.—This species is dedicated to Mr. Ph. Bruneau de Miré as a sign of appreciation for the important work done at my request on Bates' types in the Museum of Paris.

GROUP 6

Characters of the group.—Elytra black or brown, without red spots or patterns, not sericeous. Pronotum with base bordered at sides; hind angles not markedly raised; sides sinuate or subsinuate toward impunctate base; anterior submarginal border interrupted in middle.

Loxandrus depressibasis, new species

(Fig. 29a, b)

Type specimen.—*Holotype,* male (CS): R[epublica]. A[rgentina]. Tucuman Infiernillo. Specimens examined: 1.

Diagnosis.—Group 6 species characterized by the following unique combination of characters: pronotum only slightly wider than long, with depressed base (*unde nomen*); short metepisterna; proepisterna with punctures near coxae; elytra with lateral margins enlarged.

Description.—Length 9.2 mm; greatest width 3 mm. Upper surface piceous black, moderately shiny; legs, palpi, labrum and antennomere 1 ferrugineous red; lateral border and epipleuron of elytra reddish, chiefly on posterior half; antennomeres 2–11 lacking from holotype.

Head stout, slightly longer (2 mm) than wide (1.7 mm, including eyes); eyes moderately large and very slightly convex; temples long, half length of eye, very gradually convergent to neck; frontal impressions very short, nearly foveiform; front between eyes moderately convex, smooth; microsculpture indistinct at 35×.

Pronotum (Fig. 29a); length 2.05 mm; submarginal border limited to near 90° hind angles; base narrowly bordered to level of scutellum; base depressed between moderately deep and very wide impressions, inner side very gradually sloped; many short longitudinal wrinkles along base between impressions; space between impressions and hind angles convex, interrupted anteriorly by moderate oblique plica; median longitudinal line deep, with many irregular and superficial transverse wrinkles;

anterior transverse impression well marked; microsculpture present only at basal angles, but nearly indistinct at 35×.

Elytra oblong-ovate, convex; length 4.9 mm, width 3 mm; microsculpture isodiametric, very fine and dense; basal border nearly straight to slightly marked humeri and joined to lateral margin with slightly obtuse angle; sides nearly uniformly rounded to greatest width at ⅔ length; preapical sinuosity very marked; lateral margin narrow on basal half, from there obviously widened; apex of each elytron separately rounded; striae deep, nearly smooth; intervals moderately convex; puncture of interval 3 at about midlength.

Legs short; tarsomeres 5 glabrous ventrally; hind tarsomeres not carinate, short, with tarsomere 1 shorter than 5 and than 2 + 3.

Proepisterna with some scattered small punctures near coxae; angles of metasternum smooth or with few very superficial small punctures; metepisterna short, only slightly longer than anterior width, slightly punctate-rugose; sterna smooth, last one with 1 + 1 (male) setae.

Aedeagus as in Fig. 29b.

Loxandrus subsinuatus, new species

(Fig. 30)

Type specimen.—Holotype, female (MUB): Brasil Gougel [first label] Brasil [second label, green paper]. Specimens examined: 1.

Diagnosis.—Group 6 species characterized by elongate elytra ($r_d = 1.85$) and elongate head and pronotum.

Description.—Length 10.6 mm; greatest width 3.5 mm. Upper surface black, shiny, not iridescent; palpi, antennae and legs ferrugineous red, pale.

Head elongate, length 2.2 mm, width (including eyes) 1.8 mm; eyes moderately large and not very convex; temples short, very gradually convergent to neck; frontal impressions short, barely reaching level of anterior border of eyes; front between eyes convex, smooth; microsculpture indistinct at 35×. Antennae thin, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 30) convex, chiefly near anterior angles; basal angles nearly 90°, without tooth; base with very narrow border, extending to level of scutellum and with some transverse wrinkles in middle; basal impressions deep, with few faint punctures on their sides; space between impressions and hind angles smooth, convex; median longitudinal line deep, narrow, elongate, widened anteriorly; anterior transverse impression very shallow; microsculpture indistinct at 35×.

Elytra subparallel-ovate, elongate; length 6.5 mm, greatest width 3.5 mm; moderately convex; microsculpture isodiametric fine and dense; basal border slightly curved to barely rounded humeri and joined to lateral margin at obtuse angle; sides moderately and nearly uniformly curved; greatest width at midlength; preapical sinuosity very slight; apex of each elytron slightly rounded separately; striae deep, finely punctulate on disc, smooth on apical declivity; intervals convex; puncture of interval 3 at midlength.

Legs short; tarsomeres 5 glabrous ventrally; hind tarsomeres not carinate, moderately grooved on external side; hind tarsomere 1 shorter than 5 and than 2 + 3.

Underside impunctate, sericeous, microsculpture transverse, marked; metepisterna nearly twice as long as anterior width; last sternum with 2 + 2 (female) setae.

Male unknown.

GROUP 7

Characters of the group.—Elytra black or brown, without red spots or patterns, not sericeous. Pronotum with base bordered at sides; hind angles not raised; sides sinuate or subsinuate toward at least slightly punctate base; anterior submarginal border entire.

Described species.—The described species of Group 7 are divided into two sections as follows: Section A. Species having tarsomeres 5 with setae ventrally: *L. brullei* (Waterhouse) (=*argentinus* Tschitschérine) (8 mm; Fig. 32); *L. brunnescens* Straneo (6.8 mm); *L. maindroni* Tschitschérine (10–12 mm); *L. moritzi* Tschitschérine (8 mm); and *L. gravescens* Bates (7.9 mm).

Section B. Species having tarsomeres 5 glabrous ventrally: *L. minimus* Straneo

(4.2 mm); and *L. politissimus* Bates (10.1 mm). The new species described here all belong to section B, with tarsomeres 5 glabrous ventrally.

Loxandrus quadribasis, new species
(Fig. 31)

Type specimen.—Holotype, male (CS): Bolivia, Cochabamba, Chapare Alto Palmar, XI-60. Specimens examined: 1.

Diagnosis.—Group 7 (Section B) species with legs and antennae entirely ferrugineous, elytra moderately iridescent. The only similar-sized species of this group with glabrous apical tarsomeres is *L. politissimus* Bates, which is very different in that it has dark legs with only tarsomeres red, only two basal antennomeres red, and dorsal surface deep black and brilliantly iridescent.

Description.—Length 7.8 mm; greatest width 3.1 mm. Upper surface of head and pronotum blackish-brown, shiny; elytra black, shiny, moderately iridescent; antennae, mouth parts and legs pale ferrugineous. Underside blackish, shiny, moderately iridescent.

Head short, not very elongate (1.8 mm), width (including eyes) 1.5 mm; eyes large and very convex, temples very short; frontal impressions short, wide, moderately deep, reaching level of anterior border of eyes; front between eyes convex, smooth. Antennae moderately thin, elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 31) slightly convex; basal half of lateral border with row of punctures; base bordered at sides, with few very irregularly scattered punctures; basal impressions moderately elongate and deep, very wide, extending to basal angle; median longitudinal line deep and wide; anterior transverse impression very shallow.

Elytra oval, moderately convex; length 4.7 mm, greatest width 3.1 mm; microsculpture very fine and dense, isodiametric; basal border moderately curved toward very obtuse and widely rounded humeri and joined to lateral margin at obtuse angle; sides behind humeri markedly curved, from there nearly straight and divergent to greatest width at about ⅔ length; preapical sinuosity faint; apex obtusely rounded; striae moderately deep, nearly smooth; intervals slightly convex; puncture of interval 3 at about midlength.

Legs regular; tarsomeres 5 glabrous ventrally; hind tarsomeres moderately grooved on both sides; hind tarsomere 1 as long as 2 + 3; hind tarsomeres 5 lacking from holotype.

Proepisterna covered with coarse punctures; mesosternum with many faint punctures; angles of metasternum with many irregularly spaced punctures; metepisterna about 1.3 times longer than anterior width, nearly impunctate; sterna impunctate, four apical sterna with deep irregular depressions on sides; last sternum with 1 + 1 (male) setae.

I cannot give a sketch of the median lobe of the aedeagus because, though the ring is present, the aedeagus is lacking from the holotype.

Loxandrus brullei (Waterhouse)
(=*argentinus* Tschitschérine)
(Fig. 32)

The pronotum of this species (Fig. 32) is nearly identical in shape to that of *L. brunnescens* Straneo but the pronotum is differently colored. *Loxandrus brullei* (Waterhouse) is typical of a group of closely allied species characterized chiefly by shape of pronotum, which is more or less cordate and has the supramarginal anterior border markedly widened in the middle (Straneo, 1969*a*:86). This group also includes *L. brunnescens* Straneo, *L. moritzi* Tschitschérine, *L. maindroni* Tschitschérine, *L. gravescens* Bates and the following two new species.

Loxandrus fulvus, new species
(Fig. 33)

Type specimen.—Holotype, female (CMNH): Corumba, [Mato Grosso] Brazil, Acc. 2966 [first label] Jan. [second label]. Specimens examined: 1.

Diagnosis.—Group 7 (Section B) species characterized by very small size, brownish color, cordate pronotum and markedly widened anterior supramarginal border.

Description.—Length 4.9 mm; greatest width 1.9 mm. Upper surface of head blackish, with anterior part of clypeus, labrum, palpi and antennomeres 1–3 pale ferrugineous; mandibles darker; antennomeres 4–7 brown [antennomeres 8–11 lacking]; pronotum pale brown; elytra slightly darker (with exception of paler suture and apex), very markedly iridescent. Underside brown; legs pale ferrugineous.

Head very elongate; eyes large, not very convex; temples nearly absent; frontal impressions short and wide, barely reaching level of anterior margin of eyes; front between eyes convex, smooth; microsculpture indistinct at 35×. Antennae incomplete, but judging from first seven antennomeres, moderately elongate.

Pronotum (Fig. 33) slightly convex, chiefly toward base; base slightly depressed between deep impressions; space between impressions and basal angles convex, impunctate; median longitudinal line narrow, moderately impressed; microsculpture indistinct at 35×.

Elytra moderately convex, subparallel; length 2.8 mm, greatest width 1.9 mm; basal border slightly curved to slightly rounded humeri, joined to lateral margin at obtuse angle; sides behind moderate posthumeral curve nearly straight and subparallel to greatest width at ⅔ length, from there uniformly rounded to apex; preapical sinuosity moderate; striae moderately deep, nearly smooth; intervals moderately convex; puncture of interval 3 at about ⅔ length.

Legs moderately slender; tarsomeres 5 glabrous ventrally [only two tarsi remain on holotype].

Underside smooth, impunctate; metepisterna nearly twice as long as anterior width; sterna slightly depressed at sides.

Male unknown.

Loxandrus iricolor, new species
(Fig. 34a, b)

Type specimens.—Holotype, male (UASM): Brasil Amazonas, Rio Demiti ca. 0°36′N 66°57′W "La Laguna" igapo for. Sept. 13, 1978, G. E. & K. E. Ball, Brasil Exp. 1978. *Allotype,* female (UASM): same data as holotype. *Paratypes*: 5 females (CS, UASM, CMNH): same data as holotype; 1 male, 4 females (UASM, CS): Brasil, Amazonas, Rio Negro, Cucui, igapo for. Sept. 17, 1978, G. E. & K. E. Ball, Brasil Exp. 1978. Specimens examined: 12.

Diagnosis.—Group 7 (Section B) species characterized by blackish dorsal color with brownish pronotum and marked iridescence, pronotum cordate with anterior supramarginal border markedly widened in middle, ovate elytra (not subparallel), and size (similar only in *L. brunnescens* Straneo).

Description.—Length 6.7 mm; greatest width 2.5 mm. Upper surface blackish, shiny, generally markedly iridescent, especially on elytra; pronotum generally brownish; labrum, mandibles, antennae ferrugineous brown; first antennomere, palpi and legs pale ferrugineous. Underside brownish, very iridescent.

Head slightly longer (1.4 mm) than wide (1.25 mm, including eyes); eyes large and very convex; temples very short; frontal impressions deep, elongate, reaching level of anterior supraorbital seta; front between eyes convex with very fine and dense microsculpture. Antennae elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 34a); basal angles square, minutely dentate; base with few punctures, chiefly in short impressions; space between impressions and hind angles moderately convex; median longitudinal line moderate, widened between basal impressions; microsculpture indistinct at 35×.

Elytra oblong-ovate, slightly convex on disc; length 3.75 mm, greatest width 2.5 mm; microsculpture indistinct at 35×; humeri obtuse, humeral angle abruptly rounded; basal border joined to lateral margin at angle; sides gently rounded for entire length; greatest width slightly past midlength; preapical sinuosity faint; apex of each elytron blunt; striae moderately deep, impunctate; intervals nearly flat on disc; puncture of interval 3 at ⅗ length.

Legs normal; tarsomeres 5 glabrous ventrally; hind tarsomeres 1–3 carinate dorsally; hind tarsomere 1 longer than 5, about as long as 2 + 3.

Proepisterna more or less punctulate; metepisterna nearly twice as long as anterior width, punctate; angles of metasternum punctate; sterna impunctate at sides.

Aedeagus as in Fig. 34b. Shape of median lobe very unusual for *Loxandrus.*

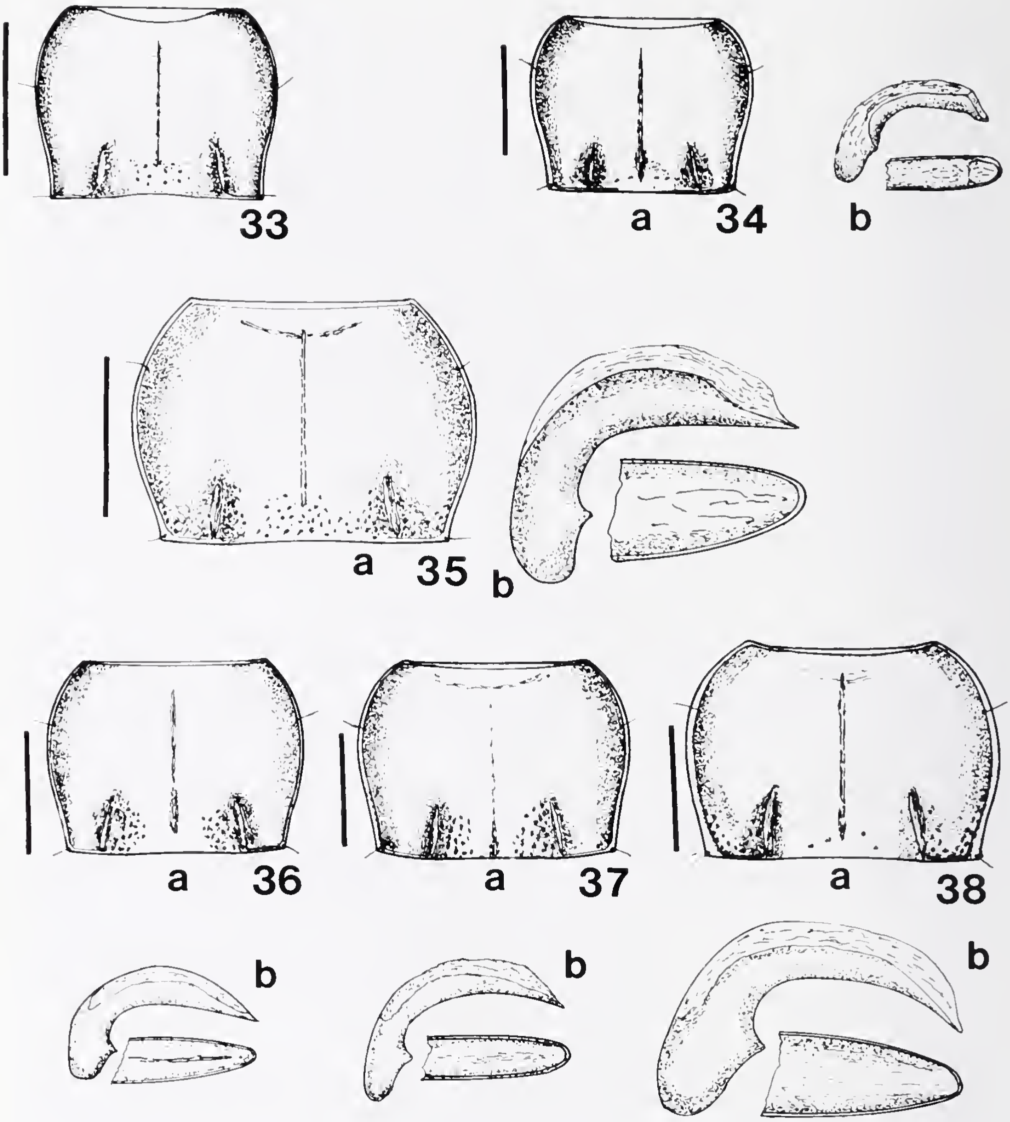

Fig. 33–38.—South American species of *Loxandrus.* Scale line = 1 mm. 33. Pronotum of *L. fulvus,* new species. 34–38.—Pronotum (a) and median lobe of aedeagus (b). 34. *L. iricolor,* new species. 35. *L. sericiventris,* new species. 36. *L. laetipes,* new species. 37. *L. affinis,* new species. 38. *L. profundestriatus,* new species.

The following new species all have the anterior submarginal border not markedly widened in middle.

Loxandrus sericiventris, new species
(Fig. 35a, b)

Type specimens.—Holotype, male (UASM): Brazil Amazonas, Rio Demiti ca. 0°40′N, 66°48′W below "Highland camp" igapo for. Sept. 11, 1978, G. E. & K.

E. Ball, Brasil Exp. 1978. *Allotype,* female (UASM): Brazil Amazonas, Rio Demiti 0°37′N, 66°48′W below "Highland camp" igapo for. Sept. 11, 1978, G. E. & K. E. Ball, Brasil Exp. 1978. *Paratype,* male (CS): same data as allotype. Specimens examined: 3.

Diagnosis.—Group 7 (Section B) species characterized by entirely sericeous ventral surface. This species is allied with *L. politissimus* Bates. The chief differences in *L. sericiventris* are that pronotum is not much narrower than elytra; pronotal hind angles are not acute and protruded; all ventral parts smooth, not punctate; dorsal color shiny black, not slightly iridescent; antennae entirely ferrugineous-brown and tibiae not dark.

Description.—Length 9.25 mm; greatest width 3.8 mm. Upper surface black, shiny; labrum brown; palpi, antennae, legs ferrugineous brown; femora slightly darker. Underside black, sericeous (*unde nomen*).

Head stout, length (1.7 mm) slightly less than width (1.9 mm, including eyes); eyes large, moderately convex, posteriorly enclosed in temples; latter ¼ eye length; frontal impressions wide, moderately deep, barely reaching level of anterior border of eyes; front between eyes convex, very shiny, without distinct microsculpture at 35×. Antennae elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 35a) slightly convex; length 1.9 mm; anterior submarginal border entire, but evanescent in middle; space between impressions with many coarse punctures; space between impressions and hind angles irregularly depressed, with few punctures only near angles; basal impressions deep, with external side very gradually inclined toward basal angles; basal angles obtuse, with tooth; median longitudinal line thin, shallow; anterior transverse impression moderate; microsculpture indistinct at 35×.

Elytra subparallel, convex; length 5.25 mm, greatest width 3.8 mm; microsculpture indistinct at 35×; humeri obtuse, rounded; basal border joined to lateral margin with obtuse curve; sides behind marked posthumeral curve subparallel for ⅗ length, from there obtusely rounded; preapical sinuosity slight; apex of each elytron moderately rounded; striae moderately deep, very finely and densely punctulate; intervals moderately convex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate on upper surface; hind tarsomere 1 as long as 5 and also as 2 + 3.

Underside entirely impunctate, sericeous; metepisterna short, 1.2 times as long as anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 35b.

***Loxandrus laetipes*, new species**

(Fig. 36a, b)

Type specimens.—*Holotype,* male (UASM): Brasil, Amazonas ca. 10 km n. e. Sao Gabriel da Cachoeira, stream margin, forest Sept. 20, 1978, Brasil Exp. G. E. Ball & K. E. Ball collectors. *Allotype,* female (UASM): same data as holotype. *Paratypes,* 3 (CS, UASM): same data as holotype. Specimens examined: 5.

Diagnosis.—Group 7 (Section B) species characterized by size, pronotal shape with anterior supramarginal border not widened in middle, marked dorsal iridescence, and shape of aedeagus.

Description.—Length 7.1 mm; greatest width 3 mm. Upper surface black with strong iridescence on pronotum and elytra; mandibles reddish; labrum, legs and antennomeres 1–3 pale ferrugineous; antennomeres 4–11 slightly darker. Underside black, partially brownish.

Head slightly wider (1.45 mm) than long (1.3 mm); eyes large, moderately convex, posteriorly enclosed in temples; latter ⅓ eye length; frontal impressions very short, deep, rounded; front between eyes convex, with very fine and dense isodiametric microsculpture. Antennae very thin and elongate, extending beyond pronotal base by four antennomeres.

Pronotum (Fig. 36a); anterior angles not blunt; basal impressions very deep and wide; space between impressions and hind angles convex, not punctate; median longitudinal line narrow, widened between impressions; microsculpture indistinct at 35×.

Elytra subparallel, moderately convex, disc nearly flat; length 4 mm, greatest width 3 mm; microsculpture very fine, scarcely distinguishable at 35×; humeri obtuse, rounded; basal border joined to lateral margin with obtuse curve; sides, behind posthumeral curve, nearly straight and parallel for ⅔ length, from there obtusely rounded; preapical sinuosity nearly absent; apex of each elytron rounded; striae deep, very densely and finely punctulate; intervals moderately convex; puncture of interval 3 coarse, slightly behind midlength.

Legs normal; tarsomeres 5 glabrous ventrally; hind tarsomeres elongate, upper side carinate; hind tarsomere 1 as long as 5 and slightly longer than 2 + 3.

Proepisterna smooth; metepisterna nearly 1.5 times as long as anterior width, nearly smooth; angles of metasternum with many coarse punctures; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 36b.

Loxandrus affinis, new species

(Fig. 37a, b)

Type specimens.—Holotype, male (UASM): Brasil, Para, Belem, Mocambo For. Preserve, igapo for., Oct. 6–8 1978, Brasil Exp. 1978. *Allotype,* female (UASM), and *paratype,* male (CS): same data as holotype. Allotype and paratype are in poor condition. Specimens examined: 3.

Diagnosis.—Group 7 species similar to *L. laetipes* (*unde nomen*), but differing in having pronotal base wider (ratio of basal width/greatest width 0.92 in *L. affinis* and 0.81 in *L. laetipes*), shorter metepisterna with coarse punctures, and row of small punctures along base of lateral border of pronotum.

Description.—Length 8.1 mm; greatest width 3 mm. Upper surface black, shiny; pronotum and elytra with lateral border reddish, markedly iridescent; labrum and mandibles brown; palpi, antennae and legs ferrugineous, first antennomere slightly paler.

Head stout, as long (1.5 mm) as wide (including eyes); eyes large and moderately convex; temples very short; frontal impressions deep, short, rounded; front smooth, convex, with very fine and dense microsculpture. Antennae very elongate, extending beyond pronotal base by four antennomeres.

Pronotum (Fig. 37a); length 1.7 mm; basal impressions deep, wide; space between impressions with few punctures at base of medial longitudinal line and many coarse punctures on inner sides of impressions; space between impressions and hind angles slightly convex, with three punctures near angles and row of small punctures along base of lateral border; anterior transverse impression shallow; microsculpture indistinct at 35×.

Elytra oblong, subparallel; disc nearly flat, slightly convex on sides and apex; length 4.75 mm, greatest width 3 mm; microsculpture nearly indistinct at 35×; humeri obtuse, rounded; basal border joined to lateral margin at obtuse angle; sides behind posthumeral curve very slightly rounded, subparallel to greatest width at ⅗ length; preapical sinuosity moderate; apex of each elytron blunt; striae deep with faint crenulations; intervals moderately convex; puncture of interval 3 at midlength.

Legs with tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 longer than 5 and longer than 2 + 3.

Proepisterna smooth; metepisterna not very elongate, 1.2 times longer than anterior width, with many coarse punctures; angles of metasternum with many coarse punctures; sterna with deep depressions on sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 37b.

Loxandrus profundestriatus, new species

(Fig. 38a, b)

Type specimens.—Holotype, male (USNM): Ecuador Napo Campana Coche e. Puerto Misahually, leaf litter hardwood swamp for. 335 m. 2.6.82 Ecuador Exp. 1982, H. E. Frania coll. *Allotype,* female (USNM), and *paratypes,* 2 males (CS, UASM): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 7 (Section B) species characterized by the combination of length (about 9 mm); black color; ovate elytra; deep and impunctate striae (*unde nomen*); ventrally glabrous apical tarsomeres. This species is wide and short, with $r_d = 2.4$.

Description.—Length 9 mm; greatest width 3.75 mm. Upper surface black, shiny, not or very slightly iridescent; labrum and mandibles pale brown; antennae, palpi and legs ferrugineous pale brown. Underside blackish, slightly shining.

Head about as long (1.6 mm) as wide (including eyes); eyes large, moderately convex; temples very short; frontal impressions deep, very short, nearly round; front smooth, convex, relatively dull, microsculpture very dense. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 38a) anteriorly very convex; length 1.7 mm; supramarginal anterior border entire and moderately widened in middle, but less than in species of *L. brullei* group dealt with above; sides very slightly subsinuate immediately before distinct basal angles (sinuation so faint that I had some doubts about whether to place this species in Group 3 or Group 7); basal impressions wide and deep; space between impressions with very few superficial, distant punctures; space between impressions and hind angles convex, with few coarse punctures on outer side of impressions and along basal part of lateral border; anterior transverse impression faint; median longitudinal line moderate, deepened anteriorly and posteriorly.

Elytra convex, ovate; length 5.5 mm, greatest width 3.8 mm; microsculpture nearly indistinct at 35×; humeri obtusely rounded; basal border joined to lateral margin without angle; sides behind posthumeral curve moderately curved, divergent to greatest width at 3/5 length, from there obtusely rounded to apex; preapical sinuosity very slight; apex of each elytron rounded; striae deep, impunctate; intervals very convex; impressed puncture of interval 3 at midlength.

Legs average; tarsomeres 5 glabrous ventrally; hind tarsomeres elongate, markedly carinate dorsally; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Proepisterna smooth; metepisterna 1.3 times as long as anterior width, smooth; angles of metasternum punctate; sterna impunctate; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 38b.

Loxandrus bonariensis, new species
(Fig. 39a, b)

Type specimen.—*Holotype,* male (CS): [Argentina:] Buenos Ayres. Specimens examined: 1.

Diagnosis.—Group 7 (Section B) species characterized by the following unique combination of characters: length 5 mm; long sinuation of sides of pronotum; entirely punctate pronotal base; and hind angles 90°.

Description.—Length 5.2 mm; greatest width 1.95 mm. Upper surface dark brown, blackish; marginal border of pronotum and apex of elytral margin reddish; antennomeres 1–3 and palpi pale ferrugineous; antennomeres 4–11 slightly darker. Underside brown.

Head small, nearly as long (1 mm) as wide (including eyes); eyes moderately large, very slightly convex; frontal impressions short and deep, barely reaching level of anterior border of eyes; temples long, slightly less than half eye length, gradually convergent behind; front between eyes smooth, moderately convex; microsculpture very fine and dense. Antennae slender, partially absent in holotype.

Pronotum (Fig. 39a); basal impressions deep, not very wide; base entirely punctate; space between impressions and hind angles not very convex, nearly flat; median longitudinal line moderate; microsculpture indistinct at 35×.

Elytra elongate, subparallel, convex; length 3.1 mm, greatest width 1.95 mm; base markedly bordered; humeri slightly convex; basal border joined to lateral margin at nearly 90°; sides after short posthumeral curve nearly straight to greatest width at 2/3 length, from there rounded to apex; preapical sinuosity moderate; striae deep, markedly punctate on disc, nearly smooth on posterior half; intervals convex; puncture of interval 3 at midlength.

Legs average; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Underside with proepisterna smooth; metepisterna twice as long as anterior width, with some punctures; angles of metasternum with some punctures; two basal sterna with few shallow punctures on sides; last sternum with 1 + 1 (male) setae.

Aedeagus as in Fig. 39b, immature.

Remarks.—The nearest allied species, *L. minimus* Straneo, has the pronotal sides briefly sinuate toward base, base punctate only in middle, body more convex and hind tarsomeres not carinate.

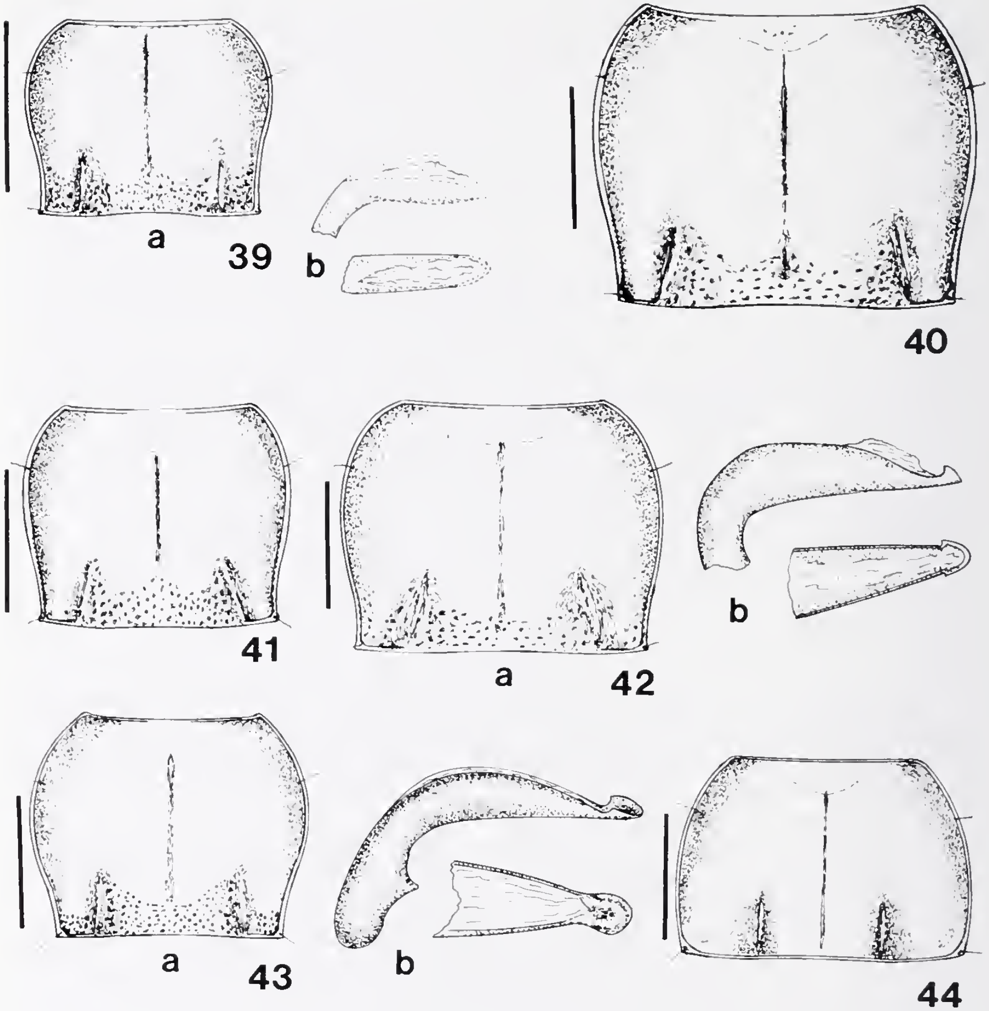

Fig. 39–44.—South American species of *Loxandrus.* Scale line = 1 mm. 39. Pronotum (a) and median lobe of aedeagus (b) of *L. bonariensis,* new species. 40, 41.—Pronotum. 40. *L. subquadratus,* new species. 41. *L. defanisi,* new species. 42, 43.—Pronotum (a) and median lobe of aedeagus (b). 42. *L. sinuatus,* new species. 43. *L. simillimus,* new species. 44. Pronotum of *L. trapezicollis,* new species.

GROUP 8

Characters of the group.—Elytra black or brown, without spots or patterns, not sericeous. Pronotum with base bordered at sides; hind angles not raised; sides sinuate or subsinuate toward more or less punctate base; anterior submarginal border interrupted in middle.

Described species.—*L. subcordicollis* Bates.

Loxandrus subquadratus, new species
(Fig. 40)

Type specimens.—*Holotype,* female (CS): Bolivia, Sta Cruz, Ichila X-62, Buena Vista. *Paratype,* female (CS): same data as holotype. Specimens examined: 2.

Diagnosis.—Group 8 species characterized by length (8 mm), darkened apical antennomeres, subrectangular pronotum with lateral border abruptly narrowed and immediately re-enlarged before basal angles, setose apical tarsomeres, and last sternum of female with only one seta on each side (only *L. defanisi* shares this character state, but *L. defanisi* is smaller with glabrous apical tarsomeres and elongate metepisterna).

Description.—Length 8 mm; greatest width 3.2 mm. Upper surface black, shiny on pronotum and elytra; lateral border of pronotum and elytra reddish; legs, palpi and antennomeres 1–4 pale ferrugineous; antennomeres 5–11 darker; mandibles and labrum pale ferrugineous. Underside blackish, slightly shiny; apical border of last sternum reddish.

Head short, triangular, slightly shorter (1.35 mm) than wide (1.5 mm, including eyes); eyes very large and convex; temples very short, nearly obsolete; frontal impressions moderately deep, narrow, short, barely reaching level of antennal insertion; front between eyes smooth and convex; microsculpture very fine and dense, isodiametric. Antennae moderately thin, extending beyond pronotal base by two or three antennomeres.

Pronotum (Fig. 40) subrectangular; length 1.95 mm; submarginal border widely interrupted in middle [in the paratype, interruption much smaller]; lateral border abruptly narrowed and immediately re-enlarged before basal angles; trace of row of small punctures on basal quarter; basal impressions wide; space between basal impressions and hind angles slightly convex, smooth; median longitudinal line thin and shallow; microsculpture indistinct at 35×.

Elytra ovate, markedly convex; length 5.1 mm, greatest width 3.2 mm; microsculpture isodiametric fine and dense; basal border slightly curved toward obtuse and widely rounded humeri, joined to lateral margin at obtuse angle; side behind moderate posthumeral curve nearly straight and subparallel to greatest width at ⅔ length, from there obtusely rounded to apex; preapical sinuosity moderate; striae deep, finely and densely punctulate; intervals moderately convex; puncture of interval 3 at midlength.

Legs normal; tarsomeres 5 with few thin setae ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 nearly as long as 5 and nearly as long as 2 + 3.

Proepisterna and metepisterna smooth; angles of metasternum and metepisterna covered with coarse and dense punctures; metepisterna short, 1.3 times as long as anterior width; sterna smooth; last sternum with only 1 + 1 (female) setae.

Male unknown.

Remarks.—This species has a puzzling combination of characters. The structure of the submarginal anterior border, which is very constant in other species, seems in this species to be exceptionally varied. In the holotype, it is very widely interrupted but in the paratype it is narrowly interrupted. More specimens are needed to establish the range of variation of this character. Moreover, the abrupt narrowing and immediate re-enlarging of the lateral pronotal border before the basal angles is unusual. Finally, the fact that the last abdominal sternum of the female bears only one seta on each side is unlike any other *Loxandrus* known to me, except *L. defanisi* described below.

The only previously described species in this group is *L. subcordicollis* Bates from the upper Amazon. Compared with it, from description, *L. subquadratus* has the pronotum less narrowed behind, not markedly cordate, and the base between impressions is covered with punctures. Also, the antennae are not entirely ferrugineous.

Loxandrus defanisi, new species
(Fig. 41)

Type specimen.—*Holotype,* female (CS): [Argentina:] Misiones-Iguazu, 30-1/13.III 45, Hayward-Willink-Colbach. Specimens examined: 1.

Diagnosis.—Group 8 species characterized by small size, glabrous apical tarsomeres, elongate metepisterna, subparallel elytra slightly convex at apex, and last sternum of female with only single seta on each side (character state shared only with *L. subquadratus,* but *L. subquadratus* is larger with setose apical tarsomeres and short metepisterna).

Description.—Length 6.5 mm; greatest width 2.5 mm. Upper surface piceous black, shiny; elytra with slight iridescence; apical part of lateral border and epipleura brown; legs, antennae, labrum and palpi pale ferrugineous; apex of mandibles slightly darker. Underside brown.

Head robust, slightly elongate; length 1.2 mm, width (including eyes) 1.3 mm; eyes moderately convex, large; temples absent; frontal impressions short, barely reaching level of anterior border of eyes; front between eyes smooth, convex; microsculpture isodiametric, scarcely distinguishable at 35 ×. Antennae mutilated in holotype.

Pronotum (Fig. 41); basal border with row of small punctures along inner line; space between angles and impressions convex, smooth; median longitudinal line moderate, short; anterior transverse impression faint; microsculpture indistinct at 35 ×.

Elytra subparallel-ovate, moderately convex; length 3.8 mm, greatest width 2.5 mm; microsculpture nearly indistinct at 35 ×; basal border nearly straight to moderately obtuse humeri and joined to lateral margin at nearly 90° angle; sides behind moderate posthumeral curve subparallel to greatest width at ⅔ length; preapical sinuosity clearly developed; apex of elytra obtusely rounded; striae deep, finely punctate; intervals moderately convex; puncture of interval 3 slightly behind midlength.

Legs average; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; tarsomere 1 nearly as long as 5 and nearly as long as 2 + 3.

Proepisterna impunctate, sericeous, microsculpture clearly marked, isodiametric; metepisterna twice as long as anterior width, with about 10 coarse punctures on anterior half; angles of metasternum covered with coarse punctures; first sternum with few moderate punctures; following sterna impunctate, with small depression on each side; last sternum with 1 + 1 (female) setae.

Remarks.—This new species is one of two known to me with only a single seta on each side of the last sternum of the female, and in that character similar to the preceding species, *L. subquadratus.* Many other characters of the two species are the same: shape of the pronotum, with a row of small punctures on the inner line; apical sternum of females with a single seta each side; color of legs. But *L. defanisi* has the apical tarsomeres glabrous ventrally, is smaller (6.5 mm instead of 8 mm), has elongate metepisterna (short in *L. subquadratus*), and has subparallel elytra slightly convex at apex.

Etymology.—Named after my grandson Giorgio De Fanis, who shows interest in my entomological studies.

Loxandrus sinuatus, new species
(Fig. 42a, b)

Type specimens.—*Holotype,* male (CMNH): Brasil, Est. Rio de Janeiro, Araruama XI.1981, Coll. M. Alvarenga. *Allotype,* female (CS), and *paratypes,* 3 females (CMNH) and a male (CS): same data as holotype. Specimens examined: 6.

Diagnosis.—Group 8 species characterized by size (nearly 8 mm), setose apical tarsomeres, markedly sulcate prosternum, characteristically shaped aedeagal apex, and last sternum of female with two setae on each side. *Loxandrus sinuatus* is nearly the same size as *L. subcordicollis* Bates but differs by less sinuate pronotum, entirely coarsely punctate pronotal base, punctulate elytral striae, and dark apical antennomeres.

Description.—Length 7.65 mm; greatest width 2.9 mm. Upper surface black (some specimens with head and pronotum slightly brownish), shiny, elytra markedly iridescent; lateral border of pronotum and elytra (chiefly at apex) more or less reddish; legs, labrum, palpi and antennomeres 1–3 pale ferrugineous, antennomeres 4–11 darker. Underside brownish black.

Head stout, slightly shorter (1.3 mm) than wide (1.45 mm), triangular; eyes moderately large, slightly convex; temples nearly absent; frontal impressions moderately impressed, barely reaching level of first supraorbital seta; front between eyes convex, smooth; microsculpture isodiametric, fine and dense. Antennae thin, slightly elongate, extending beyond pronotal base by one antennomere.

Pronotum (Fig. 42a) moderately convex, more so at anterior angles; length 1.8 mm; lateral border with some faint punctures before basal angles; basal impressions deep, slightly divergent posteriorly; space between impressions convex, with 1–6 punctures; median longitudinal line shallow, narrow; microsculpture indistinct at 35×.

Elytra oblong, convex chiefly on apical declivity; length 4.55 mm, greatest width 2.9 mm; basal border nearly straight to well marked, subdentate humeri, joined to lateral margin at obtuse angle; sides, behind posthumeral curve, very gently arcuate to greatest width at ⅔ length; preapical sinuosity moderate; striae deep, finely punctulate, third and following striae not reaching basal border; intervals moderately convex on disc, more so toward apex; puncture of interval 3 at midlength.

Legs moderately elongate; tarsomeres 5 with few thin setae ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 slightly longer than 5 and nearly as long as 2 + 3.

Prosternum deeply sulcate longitudinally; proepisterna smooth, iridescent; metepisterna and angles of metasternum covered with coarse punctures; first three sterna punctate at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus with median lobe characteristically shaped at apex (Fig. 42b).

Remarks.—Two male specimens labelled "Paraguay, Dept. Central, San Lorenzo, 18–19 Nov. 1986, J. A. Kochalka, u.v. light trap," are very similar to the type series of *L. sinuatus.* I have labelled them with this name but not included them in the paratype series.

This species, like the following one (*L. simillimus*), is one of the few *Loxandrus* having the median lobe of the aedeagus with a characteristic apex.

Loxandrus simillimus, new species
(Fig. 43a, b)

Type specimens.—Holotype, male (CMNH): Chapada, [Mato Grosso] Brazil, Acc. 2966. *Paratype,* male (CS): same data as holotype. Specimens examined: 2.

Diagnosis.—Group 8 species extremely similar to *L. sinuatus,* but with the following differences: size smaller; antennomeres 4–11 not darker than basal ones; pronotum more sinuate toward base, with base narrower and more coarsely and widely punctate; elytra shorter and with striae more markedly punctate; median lobe of aedeagus less bent and with different apical blade. The more sinuate sides of pronotum and concolorous antennae suggest *L. subcordicollis* Bates, but latter species is larger, elytral striae are not punctate, basal angles of pronotum are prominent, and pronotal base is less punctate.

Description.—Length 6.7 mm; greatest width 2.9 mm. Upper surface as in *L. sinuatus,* except all antennomeres pale ferrugineous. Underside brownish black.

Head as in *L. sinuatus.*

Pronotum (Fig. 43a); length 1.7 mm; closely similar to *L. sinuatus* except more sinuate toward base, with base narrower and more coarsely and widely punctate.

Elytral length 4.4 mm; greatest width 2.9 mm; very similar to *L. sinuatus* except slightly shorter and with striae more markedly punctate.

Legs and underside as in *L. sinuatus.*

Aedeagus (Fig. 43b) with median lobe similar to *L. sinuatus,* but less bent and with apical blade differently shaped.

With the short description of *L. simillimus* is ended the series of new species with elytra without red spots or patterns. To facilitate identification of the patterned or spotted species, I present Fig. 69–106 showing for all species the shape of the patterns on their elytra. The figures are arranged roughly in decreasing order of size of the species. As the purpose is solely to give a diagrammatic representation of the elytral pattern of each species, the figures do not include the exact shape of the elytra, or other details such as proportions, punctation of striae, shape of sides, etc. For these characters, it is necessary to consult the descriptions, chiefly in cases in which the elytral spots of two or more species are very similar.

In the descriptions, I have generally omitted characters already indicated in the key to species.

Key for Identification of Adult South American Loxandrus *with Yellow or Red Patches on Elytra*

1. Elytra with only sutural anteapical isolated rounded spot; in some specimens apical part of lateral margin of elytra reddish, but spot isolated 2

1′. Elytra with patterns or spots different from single isolated preapical sutural spot 13

2(1). Base of pronotum impunctate 3

2′. Base of pronotum more or less punctate 5

3(2). Anterior submarginal border entire (Group 9). Pronotum (Fig. 44) with greatest width toward base; size 8.6 mm; Paraguay .... *Loxandrus trapezicollis,* new species

3′. Anterior submarginal border interrupted in middle (Group 10) ... 4

4(3′). Eyes large and convex; pronotum as in Fig. 45a; spot of elytra as in Fig. 100; size 5.9 mm; Bolivia .... *Loxandrus macula,* new species

4′. Eyes large, but not very convex (Fig. 46d); pronotum as in Fig. 46a; spot of elytra as in Fig. 83; size 8 mm; Argentina .... *Loxandrus planoculis,* new species

5(2′). Anterior submarginal border entire (Group 11) 6

5′. Anterior submarginal border interrupted in middle (Group 12) ... 7

6(5). Anterior submarginal border very slightly widened in middle (Fig. 47); sides of pronotum moderately arcuate anteriorly and nearly straightly convergent to base; spot of elytra as in Fig. 87; size 7.4 mm; Santarem, Brazil .... *Loxandrus davidsoni,* new species

6′. Anterior submarginal border very much widened in middle (Fig. 48a); pronotum with sides markedly rounded for entire length; size 8 mm; spot of elytra as in Fig. 76; Paraguay .... *Loxandrus kochalkai,* new species

7(5′). Last tarsomeres glabrous ventrally; pronotum as in Fig. 49a; size 9.5 mm; elytral spot as in Fig. 70; Brazil, Amazonas .... *Loxandrus kayae,* new species

7′. Last tarsomeres with some thin setae ventrally 8

8(7′). Underside punctate; size 8–9 mm; spot of elytra as in Fig. 80; Brazil, Amazonas .... *Loxandrus rufostigma* Bates

8′. Underside impunctate, except more or less punctate metepisterna.. 9

9(8′). Hind tarsi not carinate dorsally, sulcate on external side only; spot of elytra as in Fig. 86; size 6.6 mm; Brazil, Sao Paulo .... *Loxandrus rubromaculatus* Straneo

9′. Hind tarsi sulcate on both sides; upper surface more or less carinate 10

10(9′). Size smaller, 5.7–6.5 mm; three basal antennomeres ferrugineous; metepisterna 1.5 times longer than anterior width, nearly impunctate; apex of last sternum blackish, as other sterna; sides of pronotum slightly arcuate toward base; latter distinctly wider than apex; spot of elytra as in Fig. 98; Venezuela ... *Loxandrus notula* Tschitschérine

10′. Size larger, 6.8–7.8 mm 11

11(10′). Punctation of pronotal base extended also on space between impressions and hind angles, this space moderately depressed; antennomeres 1–3 ferrugineous in most specimens; pronotum with sides moderately arcuate in anterior half, from there straight or nearly so toward base; latter distinctly wider than apex; elytra markedly iridescent; lateral border of pronotum and apical margin of elytra red; preapical sutural spot in some specimens attenuate on first interval (Fig. 85); size 7.5 mm; Venezuela .. *Loxandrus guttula* Tschitschérine

11′. Punctation of pronotal base limited to space between impressions; antennomere 1 red, 2–4 ferrugineous with blackish patch or nearly entirely blackish; femora generally partly infuscated 12

12(11′). First hind tarsomere nearly as long as fifth and as second and third together; spot of elytra small, on intervals 1–2 (Fig. 84); pronotum only slightly wider at base than apex; epipleura of elytra partly ferrugineous; size 7.8 mm; Argentina (from Tschitschérine) .... *Loxandrus posticus* Brullé

12′. First hind tarsomere nearly as long as fifth and much shorter than second and third together; spot of elytra larger, on intervals 1–3 (Fig. 101); pronotum more narrowed anteriorly, base obviously wider than apex (Fig. 50a); metepisterna nearly twice as long as anterior width, entirely impunctate, sericeous; apical margin of last sternum ferrugineous; size 6.8–7.8 mm; Paraguay .... *Loxandrus photophilus*, new species

13(1′). Elytra with red pattern formed by elongate humeral vitta extending at least on whole basal half of elytra (Fig. 73, 74, 90–96), accompanied or not by other preapical spots; anterior submarginal border of pronotum entire 14

13′. Elytra with red pattern different from above 22

14(13). Size larger (9.5–10.5 mm) 15

14′. Size smaller (5.5–7 mm) 16

15(14). Lateral red vitta narrow; preapical spots smaller (Fig. 73); length 10 mm; Brazil, Rio de Janeiro .... *Loxandrus vittatus* Bates

15′. Lateral red vitta wider; preapical patch very wide (Fig. 74); pronotum red; length 9.5 mm; Brazil, Sta. Catharina .... *Loxandrus fasciatus* Tschitschérine

16(14′). Lateral red vitta, posterior to humeral patch on sixth through eighth intervals, confined for whole length to eighth interval, joined at apex with short sutural red spot (Fig. 91); pronotum red; length 6.7 mm; Venezuela .... *Loxandrus flavicauda* Tschitschérine

16′. Lateral red vitta not confined to eighth interval; pronotum blackish, not entirely red 17

17(16′). Lateral red vitta of elytra not joined to preapical spots 18

17′. Lateral red vitta of elytra joined to preapical spots 19

18(17). Lateral red vitta of elytra longer than basal half of elytra; preapical spots as in Fig. 92; pronotum as in Fig. 51a; length 6.8 mm; Brazil, Minas Gerais .... *Loxandrus minasianus*, new species

18′. Lateral red vitta of elytra not longer than basal half of elytra; preapical spots as in Fig. 96; length 6 mm; Venezuela .... *Loxandrus interruptus* Tschitschérine

19(17′). Lateral red vitta on sixth and seventh intervals, at least on basal half 20

19′. Lateral red vitta confined to sixth interval 21

20(19). Lateral red vitta of elytra on sixth and seventh intervals for whole length of elytra, joined to wide preapical spot (Fig. 93); pronotum as in Fig. 52a; length 7 mm; Venezuela and Colombia .... *Loxandrus latifascia,* new species

20′. Lateral red vitta of elytra on sixth and seventh intervals on basal half, from there narrowed to seventh interval only (Fig. 94); length 6.5 mm; Venezuela .... *Loxandrus fasciolatus* Tschitschérine*

21(19′). Elytral preapical spot as in Fig. 90; pronotum as in Fig. 53a; length 6.5 mm; Brazil, Rio de Janeiro ... *Loxandrus janeiranus,* new species

21′. Elytral preapical spot as in Fig. 95; length 6 mm; Brazil, Sta. Catharina .... *Loxandrus subvittatus* Straneo

22(13′). Pattern of elytra formed by only two isolated spots on each elytron, first one basal, near humeri, second one (sometimes very small and indistinctly defined) preapical (Group 14) 23

22′. Pattern of elytra different (Group 15) 31

23(22). Anterior submarginal border interrupted in middle; spots of elytra as in Fig. 77; pronotum ferrugineous, with sides slightly subsinuate posteriorly; base punctate on whole width and along inner side of basal part of lateral border; length 8.3 mm; Brazil, Amazonas, Sao Paulo d'Olivenca .... *Loxandrus maculatus* Straneo

23′. Anterior submarginal border entire 24

24(23′). Apical tarsomeres with few thin setae ventrally 25

24′. Apical tarsomeres glabrous ventrally 28

25(24). Size smaller (4.8–5.1 mm); striae of elytra punctulate; spots of elytra variable (Fig. 105a, b); pronotum as in Fig. 55a; Venezuela .... *Loxandrus variabilis,* new species

25′. Size larger (7–8 mm) 26

26(25′). Striae of elytra impunctate; spots of elytra as in Fig. 72; length 7.9 mm; pronotum testaceous red; elytra very iridescent; Brazil, Obydos, lower Amazon .... *Loxandrus quadrinotatus* Bates

26′. Striae of elytra punctulate 27

27(26′). Pronotum with base impunctate; spots of elytra as in Fig. 89; length 7.2 mm; Venezuela .... *Loxandrus pictus* Tschitschérine

27′. Pronotum (Fig. 54a) with base impunctate between impressions and near angles, with row of small punctures along inner side of basal part of lateral border; size 6.9 mm; spots of elytra as in Fig. 82; Bolivia, Sta. Cruz .... *Loxandrus humeralis,* new species

28(24′). Pronotum with sides slightly subsinuate toward base (Fig. 56a); aedeagus as in Fig. 56b; spots of elytra as in Fig. 103; length 6.1 mm; Bolivia, Cochabamba .... *Loxandrus similis,* new species

28′. Pronotum with sides rounded for entire length 29

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*[Note about *L. fasciolatus* Tschitschérine. The short description of this species is evidently wrong or inexact on what refers to the pattern of elytra. The author writes "fascie jaune assez étroite, partant de l'épaule et occupant d'abord la largeur des 6-e et 7-e interstries; après le milieu elle se rétrécit sur le 6-e seul et son extrémité se réunit à une macule antéapicale légèrement oblique qui traverse les 4-e à 3-e intervalles. . . ." If the vitta is, toward the apex, on interval 6 only, it cannot join a patch on interval 4. Evidently either the preapical patch extends also on interval 5 or the apex of the vitta is on both intervals 5 and 6. An examination of the type is necessary to solve this small problem.]

29(28′). Size larger (8.3 mm); pronotum as in Fig. 57a, base obviously wider than apex; spots of elytra as in Fig. 79; striae deep, impunctate; Bolivia, Cochabamba .... *Loxandrus cribratellus,* new species

29′. Size smaller (5–6.8 mm) 30

30(29′). Base of pronotum smooth, except 2–3 punctures near hind angles (Fig. 58a); spots of elytra as in Fig. 88; length 6.8 mm; Ecuador .. .. *Loxandrus pictoides,* new species

30′. Base of pronotum with some punctures between basal impressions (Fig. 59a); spots of elytra as in Fig. 104; length 5.2–6.7 mm; aedeagus narrow and elongate (from a specimen collected in Canal Zone, Barro Colorado); Ega, upper Amazon (loc. typ.) and also Central America (Guatemala, Nicaragua) (*teste* Bates) .... *Loxandrus tetrastigma* Bates

31(22′). Pronotum with sides sinuate toward base 32

31′. Pronotum with sides rounded for entire length 33

32(31). Size larger (10.3 mm); pronotum with sides more markedly sinuate toward base and anterior submarginal border markedly widened in middle (Fig. 60a); apex of elytra with wide patches as in Fig. 69; N. Brazil, Pará .... *Loxandrus rubroniger,* new species

32′. Size smaller (6.5 mm); pronotum (Fig. 61a) with sides moderately sinuate, anterior submarginal border narrow; patches of elytra markedly reduced (Fig. 97); Argentina .. *Loxandrus sinuatellus,* new species

33(31′). Pattern of elytra formed by small humeral spot on interval 6 and partially on 5, and by transverse band at nearly ¾ length, extending on intervals 1–4 of each elytron (Fig. 71); Colombia, Ubaque, near Bogotá .... *Loxandrus ornatus* Putzeys

33′. Elytra with different pattern 34

34(33′). Elytra with only small humeral spot (Fig. 78), no other patches; pronotum as in Fig. 62; length 8 mm; Ecuador .... *Loxandrus ecuadoricus,* new species

34′. Elytra with different pattern 35

35(34′). Pattern of elytra various, as in Fig. 81a, b; pronotum as in Fig. 63a; length 7 mm; Bolivia, Chapada .... *Loxandrus nicki* Straneo

35′. Elytra without humeral spot 36

36(35′). Elytra relatively short, $r_d = 1.3$; pronotum as in Fig. 64a; size 5–6 mm; spots of elytra very small (Fig. 106); Ecuador .... *Loxandrus brevis,* new species

36′. Elytra more elongate, $r_d = 1.5$ or more; spot of elytra formed by narrow red margin joined to preapical sutural patch (Fig. 99, 102) 37

37(36′). Sutural patch round, joined with red apical margin by narrow sutural line (Fig. 102); length 6.2 mm; Brazil, Amazonas, Rio Tapajos ... . *Loxandrus picticauda* Bates

37′. Sutural patch wider, subrectangular (Fig. 99); length 6.5 mm; Brazil, Sao Paulo .... *Loxandrus elaphropus* Tschitschérine

GROUP 9

Characters of the group.—Elytra with sutural anteapical round red spot, not sericeous. Pronotum with base impunctate, bordered at base; hind angles not or very slightly raised; anterior submarginal border entire.

Loxandrus trapezicollis, new species
(Fig. 44, 75)

Type specimen.—*Holotype*, female (CS): Paraguay, [Guairá Department] Villa Rica. Specimens examined: 1.

Diagnosis.—With the characters of Group 9. The only species in the group.

Description.—Length 8.6 mm; greatest width 3.3 mm. Upper surface piceous black, shiny; elytra with very faint iridescence and preapical round red spot (Fig. 75); legs and antennomeres 4–11 brown; three basal antennomeres, palpi and tarsomeres paler.

Head moderately elongate; eyes large, convex; temples nearly absent; frontal impressions deep and wide, short, barely reaching level of anterior margin of eyes; front between eyes moderately convex. Antennae thin, elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 44) subtrapezoidal, markedly convex near anterior angles; length 1.65 mm; space between hind angles and impressions convex, to slightly depressed near hind angles; anterior transverse impression very shallow; median longitudinal line moderately deep, shortened; microsculpture indistinct at 35×.

Elytra subparallel, convex; length 4.8 mm, greatest width 3.3 mm; microsculpture indistinct at 35×; basal border very slightly curved toward obtusely rounded humeri; basal border joined to lateral margin at obtuse angle; sides, behind moderate posthumeral curve, nearly straight, very slightly divergent posteriorly; greatest width slightly behind midlength; preapical sinuosity slight; striae deep, finely punctulate; intervals moderately convex; impressed puncture of interval 3 slightly before midlength.

Legs slender, moderately elongate; tarsomeres 5 with few setae ventrally; hind tarsi elongate, tarsomeres not sulcate on inner side.

Underside entirely impunctate; metepisterna twice as long as anterior width.

Male unknown.

GROUP 10

Characters of the group.—Elytra with sutural anteapical round red spot, not sericeous. Pronotum with base impunctate, bordered at base; hind angles not raised; anterior submarginal border interrupted in middle.

Loxandrus macula, new species
(Fig. 45a, b, 100)

Type specimens.—*Holotype*, male (MUB): Bolivien, [Tarija Department] Villa Montes am R. Pilcomayo, Dr. Eisentraut S. G. 1/29-XI-30. *Paratype*, male (CS): same data as holotype. Specimens examined: 2.

Diagnosis.—Group 10 species distinguished from the only other species in the group (*L. planoculis*) by smaller size (nearly 6 mm), more convex eyes, less rounded pronotum, and details of aedeagus.

Description.—Length 5.9 mm; greatest width 2.3 mm. Upper surface black, shiny; lateral border of pronotum partly ferrugineous; elytra with slight iridescence and preapical spot (Fig. 100); apical border of elytra and apex of suture pale red; legs, palpi, labrum and antennomeres 1–3 pale ferrugineous.

Head stout; eyes large, moderately convex; temples nearly absent; frontal impressions very short, round, moderately deep; front between eyes convex, shiny, with very fine isodiametric microsculpture, visible at 35×.

Pronotum as in Fig. 45a; length 1.3 mm; basal impressions deep, narrow; basal angles subdentate; space between impressions and hind angles slightly convex, nearly flat; anterior transverse impression very shallow; median longitudinal line deep; microsculpture indistinct at 35×.

Elytra oblong, moderately convex; length 3.8 mm, greatest width 2.3 mm; basal border nearly straight to obtusely rounded humeri, joined to lateral margin at obtuse angle; sides, behind posthumeral curve, slightly and uniformly rounded to greatest width at ⅔ length; striae deep and densely punctulate, chiefly on disc; preapical sinuosity nearly absent; intervals moderately convex; puncture of interval 3 at midlength.

Legs slender; hind tarsomeres not sulcate on external side; tarsomeres 5 with few setae ventrally; hind tarsomere 1 shorter than 5, nearly as long as 2 + 3.

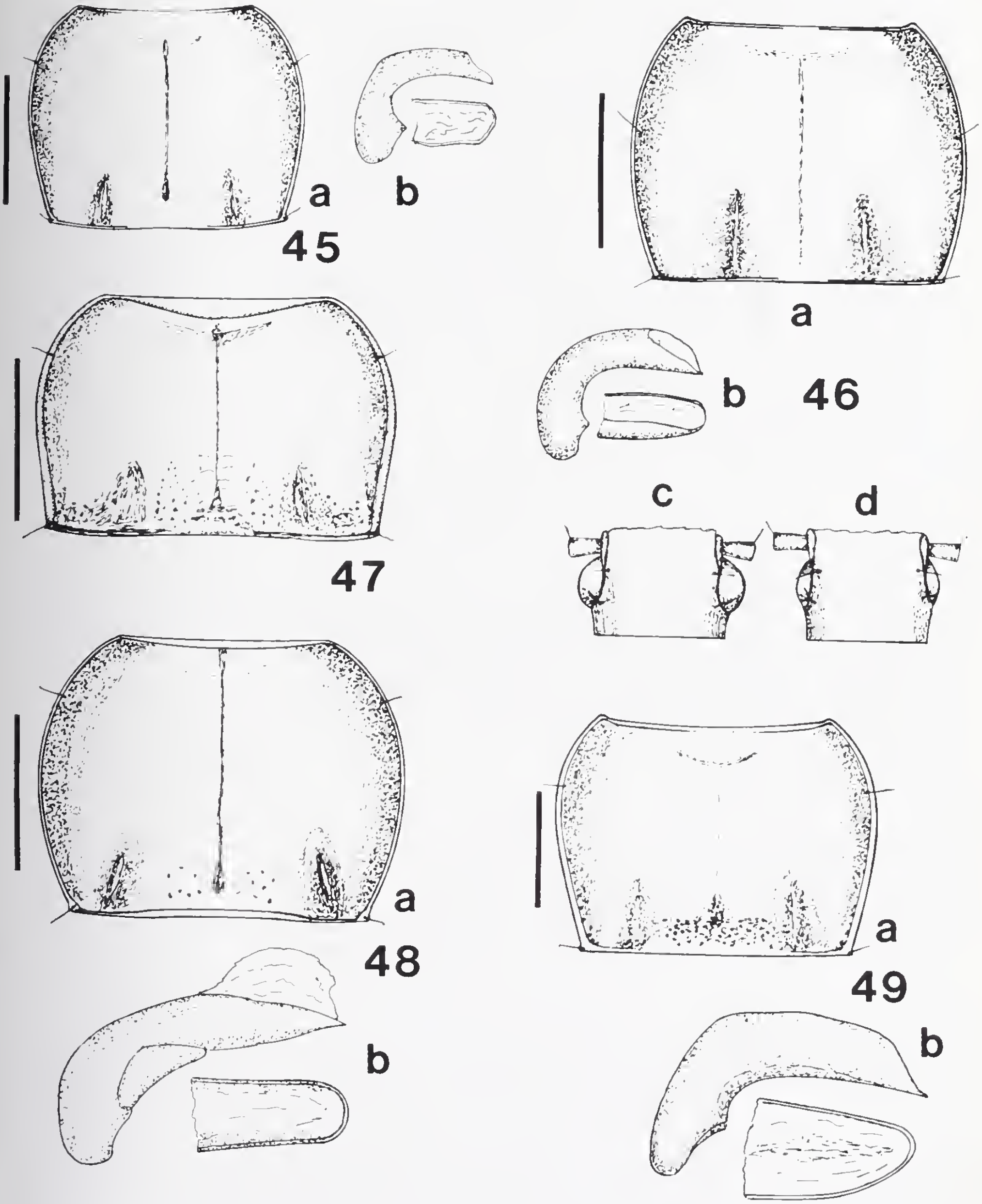

Fig. 45–49.—South American species of *Loxandrus*. Scale line = 1 mm. 45. Pronotum (a) and median lobe of aedeagus (b) of *L. macula*, new species. 46. *L. planoculis*, new species. a. Pronotum. b. Median lobe of aedeagus. c. Average convexity of eyes of *Loxandrus*. d. Relatively flat eyes of *L. planoculis*. 47. Pronotum of *L. davidsoni*, new species. 48, 49.—Pronotum (a) and median lobe of aedeagus (b). 48. *L. kochalkai*, new species. 49. *L. kayae*, new species.

Underside impunctate, sericeous; metepisterna twice as long as anterior width; sterna smooth; last sternum with 1 + 1 (male) setae.

Aedeagus as in Fig. 45b.

Loxandrus planoculis**, new species**
(Fig. 46a, b, d, 83)

Type specimens.—Holotype, male (CS): Rep[ublica]. Arg[entina]. Pronunciamiento 1-63, Prov. Entre Rios. *Allotype,* female (CS): same data as holotype. *Paratypes*: 3 (CS) and 1 (CMNH): same data as holotype; 1 (CS): Porto Alegre, Rio Grande do Sul, [Brazil] L. Buckup coll. XI.57. Specimens examined: 7.

Diagnosis.—Group 10 species distinguished from the only other species in the group (*L. macula*) by larger size (8 mm), very flat eyes, more rounded pronotum, and details of aedeagus.

Description.—Length 8 mm; greatest width 2.7 mm. Upper surface black, shiny, elytra markedly iridescent; red patch (Fig. 83) indistinctly defined, reaching apical border in some specimens; legs, antennae and palpi entirely ferrugineous red.

Head narrow, elongate; eyes not very convex (Fig. 46d, cf. Fig. 46c, average eyes of *Loxandrus*); front very convex between eyes. Antennae slender, extending beyond pronotal base by 2.5 antennomeres.

Pronotum as in Fig. 46a; basal angles with small tooth; basal border narrow; anterior transverse impression moderate; median longitudinal line very thin; microsculpture isodiametric, very fine and dense.

Elytra elongate, subparallel, convex; length 4.6 mm, greatest width 2.7 mm; basal border very slightly curved toward moderately rounded humeri and joined to lateral margin at obtuse angle; sides, behind short and slight posthumeral curve, nearly straight, subparallel; greatest width slightly past midlength; preapical sinuosity very slight; striae deep, markedly punctate for nearly ⅔ length; intervals moderately convex; puncture of interval 3 slightly before midlength.

Legs slender; tarsomeres 5 with few thin setae ventrally; hind tarsomeres carinate; hind tarsomere 1 slightly shorter than 5 and nearly as long as 2 + 3.

Underside impunctate; metepisterna nearly twice as long as anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 46b.

GROUP 11

Characters of the group.—Elytra with round, red, sutural anteapical spot, not sericeous. Pronotum punctate, bordered at base; hind angles not raised; anterior submarginal border entire, not interrupted at middle.

Loxandrus davidsoni**, new species**
(Fig. 47, 87)

Type specimens.—Holotype, male (CMNH): Santarem, [Pará] Brazil, Acc. n. 2966. *Allotype,* female (CMNH): same data as holotype [left elytron missing]. *Paratypes,* 2 males (CS, CMNH): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 11 species distinguished from the only other species in the group (*L. kochalkai*) by much shorter, more transverse pronotum, with straighter sides, wider lateral margins, narrower anterior submarginal border, and more extensively punctate base.

Description.—Length 7.4 mm; greatest width 3.4 mm. Upper surface piceous black, shiny, elytra iridescent; lateral border of pronotum reddish; elytra with lateral border, apex of epipleura and round patch (Fig. 87) ferrugineous red; antennomeres 1–3 pale ferrugineous, 4–11 dark brown; legs, palpi, and sides of labrum completely ferrugineous, pale. Ventral surface brown.

Head short, length 1.35 mm, width (including eyes) 1.6 mm; eyes large, moderately convex; temples nearly absent; frontal impressions deep, barely reaching level of anterior supraorbital seta; front between eyes convex, smooth; microsculpture isodiametric fine and dense. Antennae elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 47) very transverse; basal angles slightly obtuse, not dentate; base narrowly bordered nearly to level of scutellum, depressed between deep impressions, punctate on entire width; anterior transverse impression distinguishable; median longitudinal line faint in middle, deepened and widened at both extremities; microsculpture indistinct at 35×.

Elytra moderately convex; length 4.5 mm, greatest width 3.4 mm; basal border nearly straight to well marked, not rounded humeri, and joined to lateral margin at obtuse angle; sides, behind marked posthumeral curve, nearly straight and parallel; preapical sinuosity pronounced; striae deep, very shallowly punctulate, 5 and those following not extended to base; intervals moderately convex; impressed puncture of interval 3 slightly before midlength.

Legs average; tarsomeres 5 with few long setae ventrally; hind tarsomeres sulcate on both sides, but not carinate dorsally; hind tarsomere 1 shorter than 5 and shorter than 2 + 3.

Underside slightly sericeous; proepisterna smooth; metepisterna and angles of metasternum with some very fine and scarcely visible punctures; metepisterna nearly twice as long as anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus too immature to figure.

Etymology.—I am glad to dedicate this species to my dear friend Robert L. Davidson, who, with great patience, revised my manuscript.

Loxandrus kochalkai, new species
(Fig. 48a, b, 76)

Type specimens.—Holotype, male (CMNH): Paraguay, Dept. Central, San Lorenzo, 23/24-XI-86 (u.v. light) J. Kochalka. *Allotype,* female (CS): same data as holotype. *Paratypes*: 2 males and 2 females (CMNH), 1 male and 1 female (CS): same data as holotype. Specimens examined: 8.

Diagnosis.—Group 11 species distinguished from the only other species in the group (*L. davidsoni*) by longer, less transverse pronotum, with more-rounded sides, narrower lateral margins, wider anterior submarginal border, and less extensively punctate base.

Description.—Length 8 mm; greatest width 3 mm. Upper surface black, very shiny, not iridescent; elytra with spot (Fig. 76); legs brown red; antennae with antennomere 1 ferrugineous, 2, 3, and base of 4 brown, 5–11 black; labrum and mandibles brownish; palpi pale ferrugineous. Underside blackish.

Head robust, length 1.7 mm, width (including eyes) 2 mm; eyes large and moderately convex; temples short, continuing convexity of eyes; frontal impressions deep, subcircular, barely reaching level of antennal insertion; front between eyes very convex; microsculpture very fine, nearly indistinct at 35×. Antennae slender, elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 48a); basal angles obtuse, distinctly marked; basal impressions deep, wide, ovate; median longitudinal line irregularly impressed, extended to submarginal border; space between impressions very convex; microsculpture indistinct at 35×.

Elytra oblong, moderately convex; length 4.45 mm, greatest width 3 mm; basal border nearly straight to very obtusely rounded humeri and joined to lateral margin in curve without angle; sides from humeri to apex nearly elliptically curved; greatest width at midlength; preapical sinuosity shallow; striae deep, very closely punctate; intervals moderately convex; puncture of interval 3 at about ⅓ length.

Legs moderately elongate; tarsomeres 5 with few long setae ventrally; hind tarsomeres not carinate dorsally; hind tarsomere 1 about as long as 5 and slightly shorter than 2 + 3.

Underside entirely impunctate; metepisterna 1.5 times as long as anterior width; sterna with small depression on each side; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 48b.

Etymology.—This species is dedicated to its collector, John A. Kochalka, as recognition for collecting several new and many rare *Loxandrus.*

GROUP 12

Characters of the group.—Elytra with sutural anteapical red spot, not sericeous. Pronotum punctate, with base bordered and basal angles not raised; anterior submarginal border not entire, more or less widely interrupted in middle.

Described species.—*L. guttula* Tschitschérine (7.5 mm; Fig. 85); *L. notula* Tschitschérine (5.7–6.5 mm; Fig. 98); *L. posticus* Brullé (7.8 mm; Fig. 84); *L. rufostigma* Bates (7.9–9 mm; Fig. 80); and *L. rubromaculatus* Straneo (6.6 mm; Fig. 86). The sketches of elytral color patterns of *L. notula, L. posticus, L. rufostigma*, and *L. guttula* are based on the original descriptions.

Loxandrus kayae, new species
(Fig. 49a, b, 70)

Type specimens.—*Holotype,* male (UASM): Brasil, Amazonas, Rio Demiti, ca. 0°45′N 66°52′W, igapo for. Loc. 1, Sept. 12, 1978 Bras. Exp. 1978, G. E. & K. E. Ball coll. *Allotype,* female (UASM): same data as holotype. *Paratypes*: 1 male (CS): same data as holotype; 1 female (UASM): same data as holotype, but 0°37′N, 66°48′W, below "Highland Camp II," igapo for. Specimens examined: 4.

Diagnosis.—Group 12 species characterized by larger size and glabrous tarsomeres 5.

Description.—Length 9.5 mm; greatest width 3.6 mm. Upper surface black, shiny, elytra with faint iridescence and indistinctly defined red anteapical spot (Fig. 70); labrum and mandibles reddish brown; palpi, antennomeres 1–2 and tarsomeres pale ferrugineous, antennomeres 3–11 more or less darkened; femora dark brown; tibiae reddish brown. Underside blackish.

Head as long (1.8 mm) as wide (including eyes); eyes large, moderately convex; temples short, scarcely ⅓ eye length; frontal impressions moderately deep, not reaching level of anterior border of eyes; front convex with extremely fine isodiametric microsculpture. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 49a); anterior submarginal border interrupted in middle (faintly visible in middle in one specimen); basal angles sharp, not dentate; space between basal impressions and hind angles slightly convex, smooth except 2–3 punctures near hind angles and in some specimens along base of lateral border; median longitudinal line shallow; anterior transverse impression distinct.

Elytra subparallel, moderately convex; length 5.6 mm, greatest width 3.6 mm; microsculpture indistinct at 35×; humeri obtusely rounded; basal border joined to lateral margin with obtuse curve; sides, behind posthumeral curve, subparallel to greatest width at ⅔ length; preapical sinuosity moderate; apex of each elytron moderately rounded; striae deep, with marked punctation on basal half, from there nearly smooth; intervals moderately convex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres 1–3 shallowly carinate dorsally; hind tarsomere 1 longer than 5 and as long as 2 + 3.

Underside entirely impunctate; metepisterna twice as long as anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 49b.

Etymology.—This species is dedicated to Kathleen Elizabeth (Kay) Ball who, with her husband, collected this interesting species.

Loxandrus photophilus, new species
(Fig. 50a, b, 101)

Type specimens.—*Holotype,* male (CMNH): Paraguay, Dept. Central, San Lorenzo, 7 Nov. 1986, u. v. light, J. Kochalka. *Allotype,* female (CS), and 79 *paratypes* (CMNH, CS, UASM): same data as holotype. Specimens examined: 81.

Diagnosis.—Group 12 species characterized by following unique combination of characters: underside impunctate; hind tarsomeres sulcate on both sides; apical tarsomeres setose; hind tarsomere 1 much shorter than 2 + 3; antennomere 1 pale, antennomeres 2–11 partly or completely infuscated; size 6.8–7.8 mm.

Description.—Length 7.5 mm (6–7.6 mm); greatest width 2.7 mm. Upper surface piceous black, moderately shiny, with slight iridescence on elytra; pronotum with lateral border ferrugineous; elytra with preapical sutural spot (Fig. 101); extremity of elytra and apex of lateral border more or less ferrugineous; palpi yellow; antennomeres 1–3 ferrugineous, 2–3 more or less partially infuscated in some specimens, antennomeres 4–11 blackish; legs ferrugineous with femora of many specimens more or less infuscated. Underside dark brown.

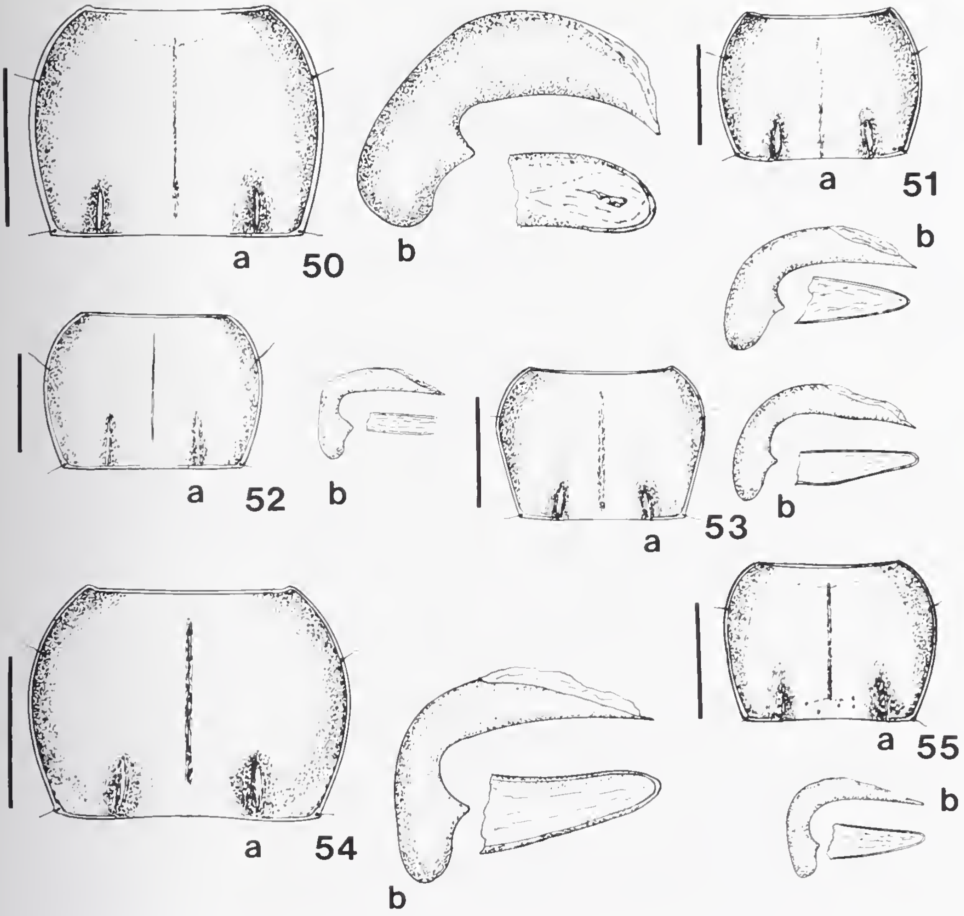

Fig. 50–55.—South American species of *Loxandrus*; pronotum (a) and median lobe of aedeagus (b). Scale line = 1 mm. 50. *L. photophilus,* new species. 51. *L. minasianus,* new species. 52. *L. latifascia,* new species. 53. *L. janeiranus,* new species. 54. *L. humeralis,* new species. 55. *L. variabilis,* new species.

Head about as long (1.45 mm) as wide (including eyes); eyes moderately convex; temples nearly absent; frontal impressions small, barely reaching level of antennal insertion; front between eyes moderately convex, with fine and dense isodiametric microsculpture.

Pronotum (Fig. 50a); basal angles with vertex not blunt; space between deep impressions and hind angles moderately convex, impunctate; median longitudinal line moderate; anterior transverse impression obsolete.

Elytra subparallel; length 4.5 mm, greatest width 2.7 mm; basal border moderately curved toward obtusely rounded humeri and joined to lateral margin at obtuse angle; sides, behind posthumeral curve, slightly curved to greatest width slightly past midlength; preapical sinuosity shallow; striae deep, impunctate; intervals moderately convex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 with few setae ventrally; hind tarsomere 1 very moderately sulcate on both sides, not carinate, slightly shorter than 5 and much shorter than 2 + 3.

Underside impunctate; metepisterna twice as long as anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 50b.

Etymology.—The name *photophilus* is proposed for this species because it was attracted in great numbers by the ultraviolet light.

GROUP 13

Characters of the group.—Elytra with red pattern formed by elongate humeral band, reaching at least midlength of elytra, in many specimens extended to ¾ length, accompanied or not by other anteapical spots, not sericeous. Pronotum with base bordered at sides; hind angles not raised.

Described species.—*L. fasciatus* Tschitschérine (9.5 mm; Fig. 74); *L. fasciolatus* Tschitschérine (6.5 mm; Fig. 94); *L. flavicauda* Tschitschérine (6.7 mm; Fig. 91); *L. interruptus* Tschitschérine (6 mm; Fig. 96); *L. subvittatus* Straneo (6 mm; Fig. 65a, b, 95); and *L. vittatus* Bates (10 mm; Fig. 73). The sketches of elytral color pattern of *L. fasciolatus, L. flavicauda* and *L. vittatus* are based on the original descriptions.

Loxandrus minasianus, new species
(Fig. 51a, b, 92)

Type specimens.—*Holotype,* male (CMNH): Brazil, Minas Gerais, Aguas Vermeilhas XII.1983, Coll. M. Alvarenga. *Allotype,* female (CS) and *paratypes,* 4 (CMNH) and 2 (CS): same data as holotype. The ninth specimen (CMNH) has the lateral vitta of elytra reduced to a fragment at the base of the sixth interval, not longer than ¼ elytra. I have referred it tentatively to this species as a color aberration. Specimens examined: 9.

Diagnosis.—Group 13 species characterized by small size (nearly 7 mm) and elytral pattern, with lateral red vitta not reaching preapical spots.

Description.—Length 6.8 mm; greatest width 2.7 mm. Head black; pronotum brown, shiny, more or less blackish; elytra (Fig. 92) shiny black with spots, lateral margin and epipleura ferrugineous red; clypeus, labrum, mandibles, palpi and antennomeres 1–3 ferrugineous; antennomeres 4–11 darker, 3 and 4 with darker apex. Underside black, not shiny.

Head as long (1.2 mm) as wide (including eyes); eyes large and moderately convex; temples nearly absent; frontal impressions moderately elongate, nearly reaching level of anterior supraorbital seta; front convex, with very fine and dense isodiametric microsculpture. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 51a); basal angles indistinctly marked; lateral border with row of punctures on basal half; space between impressions and hind angles impunctate or with 1–2 superficial punctures near angles; median longitudinal line moderate; anterior transverse impression faint; microsculpture indistinct at 35×.

Elytra subparallel, slightly convex; length 3.8 mm, greatest width 2.7 mm; microsculpture indistinct at 35×; humeri obtusely rounded; basal border joined to lateral margin without angle; sides, behind moderate posthumeral curve, nearly straight, slightly divergent to greatest width at ⅔ length, from there uniformly rounded to apex; preapical sinuosity obsolete; striae deep, nearly smooth; intervals moderately convex; puncture of interval 3 slightly past midlength.

Legs with tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 longer than 5 and nearly as long as 2 + 3.

Underside impunctate; metepisterna 1.5 times longer than anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 51b.

Loxandrus interruptus Tschitschérine
(Fig. 96)

I identified with *L. interruptus* Tschitschérine a unique male specimen in the MUB with a nearly illegible handwritten label: ". . . ? . . . dept Trabod," and a second printed label: "Paraguay leg. G. Fiebrig," because it agrees in all details with the short description. The aedeagus is very similar to that of *L. pictus* Tschitschérine (Fig. 58c).

Loxandrus fasciatus Tschitschérine
(Fig. 74)

The unique female of this species in my collection, presented in 1954 by the late Dr. G. H. Nick, is labelled: Brasilien, Nova Teutonia 27°11'S, 52°23'W Fritz Plaumann. It thus comes from the same region as Tschitschérine's type. In my opinion, *L. fasciatus* is a valid species and not, as the author supposed possible (Tschitschérine, 1900:225), a variety of *L. catharinae* Tschitschérine.

Loxandrus latifascia, new species
(Fig. 52a, b, 93)

Type specimens.—Holotype, male (USNM): Venezuela, Bolivar 8 km n. Guri 200 m 16.VII-11.VIII.1986 B. Gill. *Paratype,* male (MUB), immature: Aragua, Colomb[ia]. Montz: 23836. Specimens examined: 2.

Diagnosis.—Group 13 species characterized by small size (7 mm) and elytral pattern, with lateral red vitta on sixth and seventh intervals and joined to preapical spots (Fig. 93).

Description.—Length 7 mm; greatest width 2.5 mm. Upper surface black, shiny, not iridescent; elytra with yellow red pattern (Fig. 93); clypeus, labrum, and mandibles brown; palpi and legs pale ferrugineous; antennomeres 1–3 ferrugineous, with apex slightly darker; antennomeres 4–11 brownish.

Head as long (1.3 mm) as wide (including eyes); eyes large and moderately convex; temples nearly absent; frontal impressions short, deep, moderately wide; front convex with very fine and dense isodiametric microsculpture; antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 52a); basal angles obtuse, distinctly marked; base impunctate; row of small punctures along basal part of lateral border; median longitudinal line deep, narrow; space between impressions and hind angles slightly convex, irregular; microsculpture indistinct at 35×.

Elytra subparallel-oval, moderately convex; length 4.2 mm, greatest width 2.6 mm; humeri obtusely rounded; basal border joined to lateral margin at obtuse angle; sides, behind posthumeral curve, nearly straight and parallel to greatest width at about ⅔ length; preapical sinuosity moderate; striae deep, nearly impunctate; intervals moderately convex; puncture of interval 3 slightly past midlength.

Legs slender; tarsomeres 5 with few setae ventrally; hind tarsomere 1 sulcate on both sides, slightly carinate dorsally, very long, slightly longer than 5 and as long as 2 + 3.

Underside impunctate; metepisterna 1.5 times as long as anterior width; last sternum with 1 + 1 (male) setae.

Aedeagus elongate (Fig. 52b).

Loxandrus janeiranus, new species
(Fig. 53a, b, 90)

Type specimens.—Holotype, male (CS): Rio de Janeiro, Aranabara, Brasil 10.65 M. Alvarenga [handwritten]. *Allotype,* female (CS), and 2 *paratypes,* females (CS, CMNH): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 13 species characterized by small size (6.5 mm) and elytral pattern, with lateral red vitta confined to sixth interval and joined to preapical spot (Fig. 90).

Description.—Length 6.5 mm; greatest width 2.6 mm. Upper surface shiny, head black, pronotum dark brown, elytra black with pattern as in Fig. 90; epipleura yellow-brown; clypeus, labrum, mandibles, legs and antennomeres 1–3 ferrugineous brown (antennomeres 2 and 3 with blackish apex); antennomeres 4–11 slightly darker. Underside black, shiny; apical margin of last sternum ferrugineous.

Head nearly as long (1.1 mm) as wide (including eyes); eyes large, very convex; temples nearly absent; frontal impressions deep, wide, not very elongate; front convex with very fine and dense isodiametric microsculpture. Antennae elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 53a); basal angles marked, not blunt; space between basal impressions and hind angles various, from nearly flat with surface irregular (holotype) to moderately convex (allotype and paratypes); median longitudinal line deep and wide; microsculpture indistinct at 35×.

Elytra subparallel-oval; length 4.1 mm, greatest width 2.6 mm; disc moderately convex; humeri very obtuse, rounded; basal border joined to lateral margin with very short curve; sides behind marked posthumeral curve nearly straight, slightly divergent to greatest width at ⅓ length, from there uniformly rounded to apex; preapical sinuosity shallow; apex of each elytron blunted, neither rounded nor sharp; striae deep, nearly smooth; intervals convex; puncture of interval 3 at midlength.

Legs moderately slender; tarsomeres 5 glabrous ventrally; hind tarsomeres moderately grooved on both sides, not carinate; hind tarsomere 1 much longer than 5 and as long as 2 + 3.

Underside wholly impunctate, except angles of metasternum with few moderate punctures; metepisterna more than 1.5 times longer than anterior width; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 53b.

GROUP 14

Characters of the group.—Each elytron with two separate small spots, one humeral and one preapical (but not sutural), not sericeous. Pronotum with base bordered at sides; basal angles not raised.

Described species.—*L. maculatus* Straneo (8.9 mm; Fig. 77); *L. quadrinotatus* Bates (7.9 mm; Fig. 72); *L. pictus* Tschitschérine (7.2 mm; Fig. 58c, 89); and *L. tetrastigma* Bates (8.3 mm; Fig. 59, 104).

Loxandrus variabilis, new species
(Fig. 55a, b, 105a, b)

Type specimens.—*Holotype,* male (USNM): Venezuela, Bolivar, 8 km n. Guri 200 m, 16.VII–11.VIII.1986, B. Gill. *Allotype,* female (CS), and 17 *paratypes* (UASM, CS, CMNH): same data as holotype. Specimens examined: 19.

Diagnosis.—Group 14 species characterized by small size (4.8–5.1 mm), setose apical tarsomeres, and anterior submarginal border of pronotum entire.

Description.—Length 5.2 mm (4.8–5.7 mm); greatest width 2.3 mm. Color of upper surface various according to maturity. In fully mature specimens, head is shiny black; pronotum blackish brown; elytra black with spots as in Fig. 105, size of spots various, from most (Fig. 105b) to least (Fig. 105a) extensive; clypeus, labrum and mandibles, and antennomere 1 ferrugineous; antennomeres 2–3 ferrugineous with blackish apex; antennomeres 4–11 more or less darker; palpi and legs pale ferrugineous. Underside blackish, shiny.

Head nearly as long (1.3 mm) as wide (including eyes); eyes large and convex; frontal impressions deep, wide, barely reaching level of anterior border of eyes; temples nearly absent; front convex, with nearly indistinct fine and dense isodiametric microsculpture. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 55a); basal angles obtuse, not blunt; space between basal impressions with few punctures, very varied in number and depth, extending also along basal part of lateral border; median longitudinal line thin; anterior transverse impression visible in some specimens, indistinct in others; microsculpture indistinct at 35×.

Elytra subparallel-oval, moderately convex; length 3.5 mm, greatest width 2.3 mm; humeri moderately obtuse; apex of each elytron blunted; basal border joined to lateral margin at moderately obtuse angle; sides nearly uniformly curved for entire length; greatest width at about ⅔ length; preapical sinuosity faint; striae very deep, moderately punctulate; intervals convex; puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 with 2–3 very thin setae ventrally; hind tarsomeres 1–3 carinate dorsally; hind tarsomere 1 subequal to 5 and to 2 + 3.

Underside iridescent; proepisterna with many punctures on inner part; metepisterna relatively short, 1.3 times as long as anterior width, densely punctulate, also angles of metasternum and sides of abdominal sterna; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 55b.

Remarks.—Specimens of this species with very wide spots resemble those of *L. ornatus* Putzeys, from which they differ by much smaller size with ventral surface densely punctulate. Many of the paratypes are damaged. The holotype has the widest elytral pattern. Most of the paratypes have reduced spots.

Loxandrus pictus Tschitschérine

(Fig. 58c, 89)

This species was described from a single specimen from Valencia, Venezuela. In the collection of the Museum of Berlin, there is a series of six *Loxandrus* which agree more or less with Tschitschérine's description. I have determined them, with some question, as *Loxandrus pictus* Tschitschérine. One of them is labelled "Caracas, O. Thieme." The remaining specimens are labelled "Columbia Muntz."

Loxandrus humeralis, new species

(Fig. 54a, b, 82)

Type specimens.—*Holotype,* male (MLM): Bolivia, Sta Cruz Est. Experimental Gral. Saavedra VI. 1974 L. Stanger—C. Porter. *Allotype,* female (MLM), and 2 *paratypes* (CS): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 14 species characterized by larger size (nearly 7 mm), setose apical tarsomeres, punctulate elytral striae, pronotum with anterior submarginal border entire and row of small punctures along inner side of basal part of lateral border.

Description.—Length 6.9 mm; greatest width 2.8 mm. Upper surface dark brown, moderately shiny; lateral border of pronotum and elytra reddish; pattern of elytra as in Fig. 82; legs, palpi and antennomeres 1–3 pale ferrugineous, antennomeres 4–11 darkened. Underside blackish, iridescent.

Head subtriangular, short; eyes large, convex; frontal impressions moderately impressed, barely reaching level of anterior border of eyes; temples nearly absent; front between eyes moderately convex. Antennae moderately elongate, extending beyond pronotal base by one antennomere.

Pronotum (Fig. 54a); length 1.4 mm; basal angles obtuse, not rounded; lateral border with row of more or less deep punctures; space between impressions and angles flat or slightly depressed, generally impunctate; median longitudinal line wide and deep; microsculpture indistinct at 35×.

Elytra subparallel, disc slightly convex; length 4.1 mm, greatest width 2.8 mm; microsculpture nearly indistinct at 35×; humeri obtuse, blunt; basal border joined to lateral margin without angle; sides, behind posthumeral curve, nearly straight, slightly divergent to greatest width at ⅔ length; preapical sinuosity moderate; striae deep, very finely punctulate; intervals moderately convex; puncture of interval 3 at ⅗ length.

Legs moderately slender; tarsomeres 5 with 2–3 very thin, scarcely visible setae ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 slightly longer than 5 and as long as 2 + 3.

Underside with proepisterna impunctate; mesosternum and angles of metasternum nearly impunctate; metepisterna 1.5 times longer than anterior width.

Aedeagus as in Fig. 54b.

Loxandrus similis, new species

(Fig. 56a, b, 103)

Type specimens.—*Holotype,* male (USNM): Bolivia, Cochabamba, Villa Tunari, for. leaf litter 430 m May 1979, H. Frania coll. *Allotype,* female (USNM): same data as holotype. *Paratypes*: 2 (CS), 1 (UASM): same data as holotype; 1 (UASM): Bolivia Cochabamba between Corani and Villa Tunari, ex canopy small fallen tree 1180 m, May 28, 1979 H. Frania coll. Specimens examined: 6.

Diagnosis.—Group 14 species characterized by glabrous apical tarsomeres, pronotum with anterior submarginal border entire and sides subsinuate toward base.

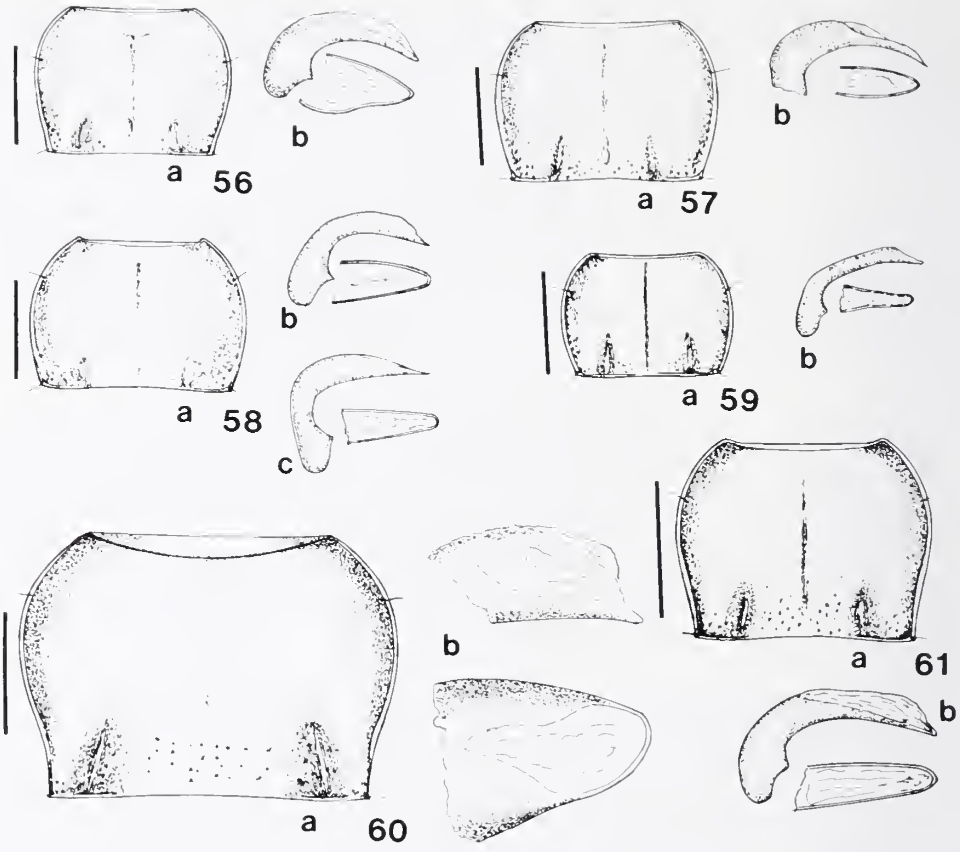

Fig. 56–61.—South American species of *Loxandrus*. Scale line = 1 mm. 56, 57.—Pronotum (a) and median lobe of aedeagus (b). 56. *L. similis,* new species. 57. *L. cribratellus,* new species. 58. a. Pronotum of *L. pictoides,* new species. b. Median lobe of aedeagus of *L. pictoides.* c. Median lobe of aedeagus of *L. pictus* Tschitschérine for comparison. 59–61.—Pronotum (a) and median lobe of aedeagus (b). 59. *L. tetrastigma* Bates. 60. *L. rubroniger,* new species. 61. *L. sinuatellus,* new species.

Description.—Length 6.1 mm; greatest width 2.6 mm. Upper surface black, shiny, elytra moderately iridescent and with pattern as in Fig. 103; clypeus, labrum, palpi, antennae and trochanters ferrugineous, more or less pale. Underside blackish brown, shiny.

Head slightly wider than long (1.1 mm); eyes very large, convex; temples very short, nearly absent; frontal impressions small, deep, round; front convex, with very fine and dense thin isodiametric microsculpture, scarcely distinct at 35×. Antennae moderately elongate, extending beyond pronotal base by one antennomere.

Pronotum (Fig. 56a); basal angles sharp, not dentate; space between impressions and hind angles slightly depressed with many coarse punctures extending on basal part of lateral border; median longitudinal line widened and deepened posteriorly; microsculpture not distinguishable at 35×.

Elytra ovate, nearly flat on disc, moderately convex at apex; length 4 mm, greatest width 2.6 mm; humeri obtuse, rounded; basal border joined to lateral margin at angle; sides nearly uniformly arcuate for entire length; preapical sinuosity moderate; apex of each elytron separately rounded; striae deep, finely crenulate; intervals moderately convex; puncture of interval 3 at midlength.

Legs with tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 longer than 5 and as long as 2 + 3.

Underside with proepisterna iridescent; metepisterna nearly twice as long as anterior width, smooth or very slightly punctulate; angles of metasternum with many superficial punctures; sterna depressed at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 56b.

Loxandrus cribratellus, new species
(Fig. 57a, b, 79)

Type specimens.—Holotype, male (USNM): Bolivia, Cochabamba, Villa Tunari, ex fruitfall 430 m, May 12, 1979 H. Frania coll. *Allotype,* female (USNM), and *paratype,* female (CS): same data as holotype. Specimens examined: 3.

Diagnosis.—Group 14 species characterized by larger size (8.4 mm), apical tarsomeres glabrous ventrally, pronotum with anterior submarginal border entire and sides rounded to base.

Description.—Length 8.4 mm; greatest width 3.25 mm. Upper surface of head and elytra blackish, of pronotum brown; elytra markedly iridescent with color pattern as in Fig. 79; clypeus, labrum, palpi and legs with trochanters pale ferrugineous. Underside brownish.

Head slightly longer (1.9 mm) than wide (1.55 mm, including eyes); eyes large and convex; temples very short; frontal impressions moderately deep, short, reaching level of antennal insertion; front convex, with fine and dense thin isodiametric microsculpture, scarcely distinguishable at 35×. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 57a); length 1.55 mm; basal angles sharp, not dentate; space between impressions and hind angles with many coarse punctures, chiefly near angles, extending along basal part of lateral border; median longitudinal line narrow, deep; anterior transverse impression moderate, short; microsculpture indistinct at 35×.

Elytra very moderately convex; length 5.15 mm, greatest width 3.25 mm; humeri very obtusely rounded; basal border joined to lateral margin without angle; sides nearly uniformly curved for entire length; greatest width at nearly ¾ length; preapical sinuosity very faint; striae moderately deep, not punctulate; intervals slightly convex; puncture of interval 3 slightly behind midlength.

Legs with tarsomeres 5 glabrous ventrally (holotype and paratype with incomplete hind tarsi, but allotype has all tarsomeres 5 glabrous); hind tarsomere 1 not or very slightly sulcate on external side only; hind tarsomere 1 longer than 5 and than 2 + 3.

Underside with proepisterna smooth; metepisterna narrow, twice as long as anterior width, nearly smooth or with few very small punctures; angles of metasternum densely punctate; sterna impunctate with irregular impressions at sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 57b.

Loxandrus pictoides, new species
(Fig. 58a, b, 88)

Type specimens.—Holotype, male (USNM): Ecuador Napo km 24 n. Cotundo Tena-Baez rd. Fruitfall H. E. Frania & F. A. H. Sperling coll. May 1, 1982. *Allotype,* female (USNM): Ecuador Napo Campana Cocha, e. Puerto Misahualli, fruitfall 335 m, 31.V.82, H. E. Frania coll. *Paratypes*: male (CS): same data as allotype; male (UASM): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 14 species characterized by smaller size (6.8 mm), apical tarsomeres glabrous ventrally, pronotum with anterior submarginal border entire, sides rounded to base, base impunctate between basal impressions.

Description.—Length 6.8 mm; greatest width 2.75 mm. Upper surface blackish brown, shiny, slightly iridescent; pattern of elytra as in Fig. 88 (spots reduced in one paratype, preapical spot nearly absent); apical border of elytra narrowly reddish; clypeus, labrum and mandibles reddish brown; antennae, palpi, legs and trochanters pale ferrugineous. Underside blackish brown, apical border of last sternum ferrugineous.

Head nearly as long (1.2 mm) as wide (including eyes); eyes large and convex; temples nearly absent; frontal impressions shallow, wide, short, barely reaching level of antennal insertion; front convex, smooth; microsculpture indistinct at 35×. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum moderately convex (Fig. 58a); lateral channel very shallow, especially toward base; length

1.5 mm; space between impressions various, from nearly impunctate to shallowly and sparsely punctate only on inner side of impressions; space between impressions and hind angles various and irregular, impunctate except 3–4 small punctures near hind angle; median longitudinal line deep, wide; anterior transverse impression faint; microsculpture indistinct at 35×.

Elytra oblong, ovate, slightly convex on disc, more so toward apex; length 4.1 mm, greatest width 2.75 mm; humeri obtusely angled, neither rounded nor dentate; basal border joined to lateral margin with angle; sides nearly uniformly curved for entire length; greatest width about midlength; preapical sinuosity faint; striae deep, impunctate or nearly so; intervals convex; puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 longer than 5 and as long as 2 + 3.

Underside iridescent; proepisterna smooth; metepisterna 1.5 times longer than anterior width, impunctate or nearly so; angles of metasternum with many coarse punctures; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 58b (cf. Fig. 58c: median lobe of *L. pictus* Tschitschérine).

Remarks.—A male specimen (UASM) labelled "Ecuador Napo Puerto Misahually, leaf litter, flower fall, 366 m, 30-V-82 H. E. Frania coll," seems to belong to this species, but the striae are distinctly punctulate and the basal angles and the basal part of the lateral border of pronotum are coarsely punctulate. Probably it is an aberrant specimen. Therefore I labelled it "?*pictoides*" but did not include it in the type series.

Loxandrus tetrastigma Bates
(Fig. 59a, b, 104)

Bates described this species from Ega, Upper Amazon. In Biologia Centrali Americana, he illustrated (1882: table IV, fig. 13) the same species and wrote (p. 87) "Hab. Guatemala, Zapote (Champion); Nicaragua, Chontales (Belt).—South America, Upper Amazons." If the specimens from Central America are really conspecific with those from the Amazon, *L. tetrastigma* has a very wide distribution. The sketches in this paper (Fig. 59 and 104) are drawn from specimens in my collection from Barro Colorado Island, Panamá, which agree entirely with Bates' description.

GROUP 15

Characters of the group.—Elytra with pattern different from that of groups 13 and 14, not sericeous. Pronotum with base bordered at sides; basal angles not or very slightly raised.

Described species.—*L. elaphropus* Tschitschérine (6.5 mm; Fig. 99); *L. nicki* Straneo (7 mm; Fig. 63a, b, 81a, b); *L. ornatus* Putzeys (9.5 mm; Fig. 71); and *L. picticauda* Bates (6 mm; Fig. 102).

Loxandrus rubroniger, new species
(Fig. 60a, b, 69)

Type specimen.—*Holotype,* male (MUB): Nord Brasilien [Brazil], Para [State]. Saure Marajo, O. Berthram S. V. Specimens examined: 1.

Diagnosis.—Group 15 species characterized by larger size (10.3 mm), sinuate sides of pronotum, and anterior submarginal border of pronotum markedly widened in middle.

Description.—Length 10.3 mm; greatest width 4.1 mm. Upper surface black, slightly shining; pattern of elytra as in Fig. 69; epipleura and apical part of lateral border of elytra reddish; palpi and antennomere 1 pale ferrugineous; antennomeres 2–11 dark brown, chiefly at apex; legs and trochanters dark reddish brown.

Head nearly as long (2.2 mm) as wide (including eyes); eyes large and moderately convex; temples nearly absent; frontal impressions deep, moderately wide, short, barely reaching level of anterior border of eyes; front between eyes little convex, smooth; microsculpture indistinct at 35×. Antennae thin, elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 60a) markedly convex anteriorly, slightly convex at base; basal impressions deep; space between impressions and hind angles slightly convex with 2–4 punctures near hind angles; lateral border evanescent slightly before base; median longitudinal line moderate and very short; microsculpture indistinct at 35×.

Elytra subparallel, moderately convex on disc, more so toward apex; length 6.4 mm, greatest width 4.1 mm; microsculpture fine and dense, isodiametric; humeri very obtuse and obtusely rounded; basal border slightly curved, joined to lateral margin without angle; sides behind posthumeral curve nearly straight to greatest width at about ¾ length; preapical sinuosity moderate; striae deep, very finely and densely punctulate; intervals slightly convex for entire length; puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 with some long setae ventrally; hind tarsomeres markedly sulcate on external side, not carinate; hind tarsomere 1 shorter than 5 and shorter than 2 + 3.

Underside entirely impunctate; metepisterna 1.5 times longer than anterior width; sterna not depressed on sides; last sternum with 1 + 1 (male) setae.

Aedeagus (Fig. 60b) very immature.

Loxandrus sinuatellus, new species
(Fig. 61a, b, 97)

Type specimens.—Holotype, male (CS): Cayasta, R[epublica]. Argentina, juil aout 96. *Paratype,* male (CS): same data as holotype. Specimens examined: 2.

Diagnosis.—Group 15 species characterized by smaller size (6.5 mm), sinuate sides of pronotum, and anterior submarginal border of pronotum narrow.

Description.—Length 6.5 mm; greatest width 2.4 mm. Upper surface blackish brown, shiny, iridescent on elytra; lateral border of pronotum, apical half of elytral margin and sutural interval brown (Fig. 97); antennae and legs pale ferrugineous. Underside brown, with mentum and apex of abdomen paler.

Head small, not elongate; eyes very moderately convex; temples short; frontal impressions very short, wide, barely reaching level of antennal insertions; front between eyes convex, smooth, with very fine and dense isodiametric microsculpture.

Pronotum (Fig. 61a); basal angles 90°; basal impressions wide, deep; median longitudinal line deep and wide; microsculpture indistinct at 35×.

Elytra subparallel, moderately convex; length 3.6 mm, greatest width 2.4 mm; microsculpture indistinct at 35×; basal border markedly curved to abruptly rounded humeri and joined to lateral margin at nearly 90° angle; sides slightly arcuate to greatest width at about ⅔ length; preapical sinuosity nearly absent; striae deep, very finely punctulate on disc; intervals convex; puncture of interval 3 at midlength.

Legs with tarsomeres 5 glabrous ventrally; hind tarsomeres carinate dorsally; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Underside with proepisterna smooth; metepisterna about 1.5 times longer than anterior width, coarsely punctate; sides of metasternum coarsely punctate; first sternum irregularly depressed on sides; last sternum with 1 + 1 (male) setae.

Aedeagus as in Fig. 61b.

Loxandrus ecuadoricus, new species
(Fig. 62, 78)

Type specimens.—Holotype, female (CMNH): Ecuador, Carchi, Chical, 1250 m, 0°56′N 78°11′W, coll. R. Davidson VII.3–10.1983. *Paratypes,* 3 females (CMNH, CS): same data as holotype, but two specimens with a second label: Ex Eleocharis elegans swamp. Specimens examined: 4.

Diagnosis.—Group 15 species characterized by pronotum, with sides rounded to base, and elytral pattern, with only small humeral spot on each elytron.

Description.—Length 8 mm; greatest width 3.3 mm. Upper surface black, shiny, elytra (Fig. 78) with humeral band and epipleura ferrugineous; legs, antennae, labrum and palpi pale ferrugineous.

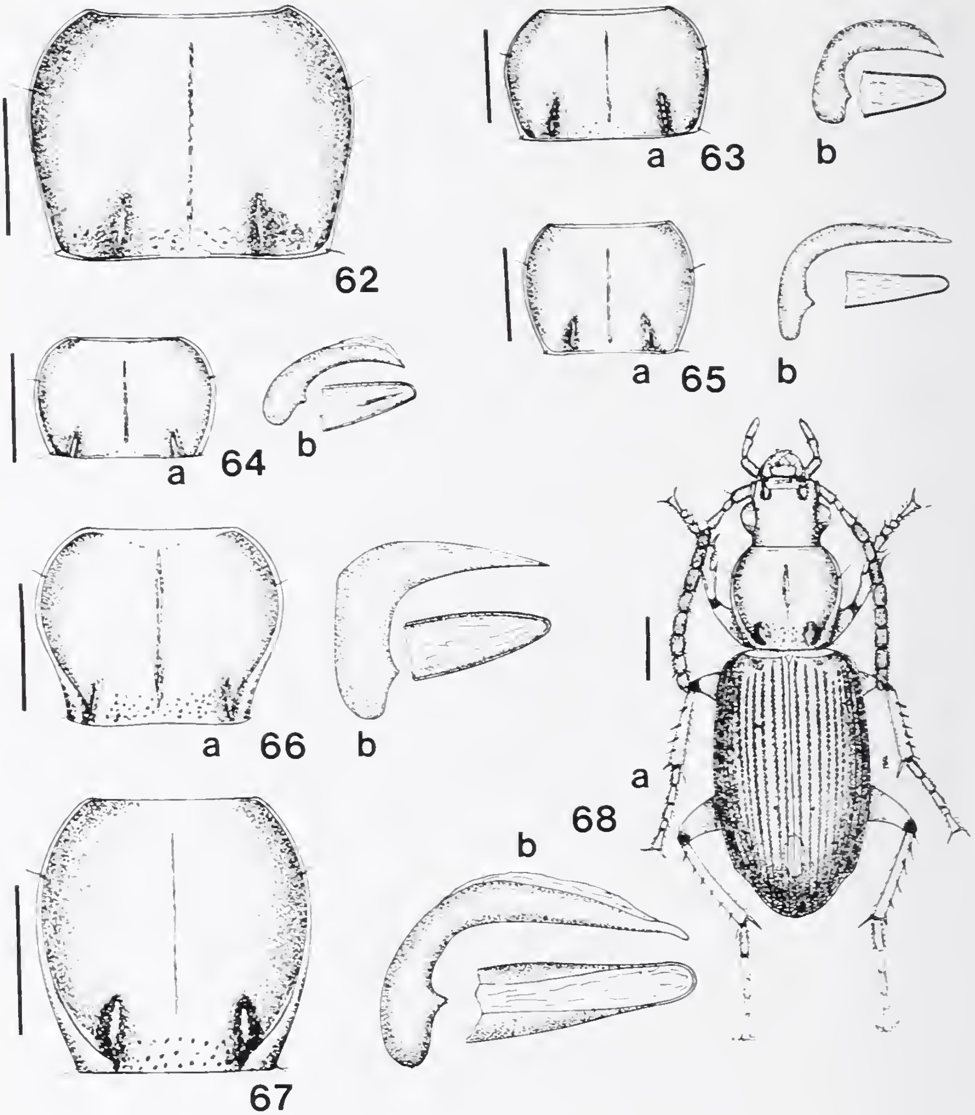

Fig. 62–68.—South American species of *Loxandrus*. Scale line = 1 mm. 62. Pronotum of *L. ecuadoricus*, new species. 63–66.—Pronotum (a) and median lobe of aedeagus (b). 63. *L. nicki* Straneo. 64. *L. brevis*, new species. 65. *L. subvittatus* Straneo. 66. *L. reflexicollis*, new species. 67. Pronotum of *L. attenuatus* Bates. 68. Habitus (a) and median lobe of aedeagus (b) of *L. ornatellus*, new species.

Head as long (1.5 mm) as wide (including eyes); eyes large and convex; temples nearly absent; frontal impressions extending anteriorly on clypeus, very short posteriorly; front convex; microsculpture fine and dense, isodiametric.

Pronotum (Fig. 62); lateral border with row of punctures posteriorly; basal impressions wide, irregular, chiefly on external side; space between impressions and hind angles with irregular depression and few punctures; median longitudinal line wide, irregular; microsculpture indistinct at 35×.

Elytra subparallel, moderately convex; length 4.8 mm, greatest width 3.3 mm; microsculpture indistinct at 35×; basal border slightly curved toward widely rounded humeri and joined to lateral margin in wide curve; side, behind posthumeral curve, slightly arcuate to greatest width at ⅔ length; preapical sinuosity nearly absent; striae moderately deep, nearly smooth; intervals slightly convex, nearly flat; puncture of interval 3 at midlength.

Legs slender; tarsomeres 5 glabrous ventrally; hind tarsomeres sulcate on external side; hind tarsomere 1 slightly longer than 5 and slightly longer than 2 + 3.

Underside impunctate, iridescent; metepisterna very narrow, about 1.5 times longer than anterior width; last sternum with 2 + 2 (female) setae.

Male unknown.

Loxandrus nicki Straneo
(Fig. 63a, b, 81a, b)

In the description of this species (Straneo, 1955:147), I pointed out the great variability of the elytral pattern, even in specimens from the type locality: Bolivia, Reg. Chapara. In specimens borrowed from Dr. Ball (UASM), I found four specimens of this species from Bolivia, Cochabamba, Villa Tunari, 430–450 m, May 1979, H. Frania coll., and 23 specimens from Ecuador, Napo, Campana Cocha, e. Puerto Misahualli, fruitfall, 335 m, 31.V.82, H. Frania coll. From both localities there are specimens with complete pattern (Fig. 81a) and with reduced spot (Fig. 81b), and specimens intermediate between the two patterns. I do not find other differences between the two forms, so I think that the specimens with reduced patterns are no more than individual aberrations. I emphasize this variation to avoid having these aberrations described as a valid species, and to avoid having them confused with *L. humeralis* (Group 14). *Loxandrus humeralis* is similar, but differs in the shape of the pronotum (much more transverse in *L. nicki*) and of the median lobe of the aedeagus (much shorter posterior to the basal bend in *L. nicki*) (Fig. 54 and 63).

Loxandrus brevis, new species
(Fig. 64a, b, 106)

Type specimens.—Holotype, male (USNM): Ecuador, Napo, Campana Cocha: e. Puerto Misahualli, fruitfall, 335 m. 31.V.82 H. E. Frania coll. *Allotype,* female (USNM), and 2 *paratypes,* females (CS, UASM): same data as holotype. Specimens examined: 4.

Diagnosis.—Group 15 species characterized by pronotum with sides rounded to base, elytra short, elytral pattern lacking humeral spot and having relatively small apical spots.

Description.—Length 5.6 mm (5–6 mm); greatest width 2.8 mm. Upper surface black, shiny, not or very slightly iridescent; elytra with diffuse pattern as in Fig. 106; clypeus, labrum, mandibles, legs and antennomere 1 pale ferrugineous; antennomeres 2–11 pale brown, partially darkened at apex. Underside blackish, iridescent; apical margin of last sternum brown.

Head as long (1.1 mm) as wide (including eyes); eyes large and moderately convex; temples very short; frontal impressions deep, short, barely reaching level of antennal insertion; front smooth, with fine and dense microsculpture, scarcely distinct at 35×. Antennae moderately elongate, extending beyond pronotal base by two antennomeres.

Pronotum (Fig. 64a); basal angles with vestigial tooth; basal impressions short, moderately to very deep; some coarse punctures near hind angles and along inner side of lateral border; space between impressions and hind angles not depressed; median longitudinal line moderately impressed; microsculpture indistinct at 35×.

Elytra slightly convex, oval, short, wide; length 3.7 mm, greatest width 2.8 mm; microsculpture indistinct at 35×; humeri very obtusely rounded; basal border joined to lateral margin at obtuse angle; sides moderately and uniformly curved to greatest width at about ¾ length, from there markedly rounded to widely obtuse apex; preapical sinuosity moderate; striae deep, coarsely punctate; intervals convex; puncture of interval 3 behind midlength.

Legs not very elongate; tarsomeres 5 glabrous ventrally; hind tarsomeres moderately carinate dorsally; hind tarsomere 1 longer than 5 and as long as 2 + 3.

Proepisterna with some punctures on inner side near coxae; metepisterna about twice as long as anterior width, with few punctures on inner side, more numerous and coarser on angles of metasternum; sterna more or less depressed on sides; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

Aedeagus as in Fig. 64b.

Etymology.—This is a very short and broad species, *unde nomen.*

GROUP 16

Characters of the group.—Base of pronotum bordered at sides; basal angles not raised. Upper surface black, not or slightly shiny on head and pronotum; elytra sericeous opaque, with marked isodiametric microsculpture.

Described species (all about 6–7 mm in length).—*L. negrei* Straneo 1967; *L. opaculus* Bates 1871; and *L. sericeus* Straneo 1955.

Loxandrus negrei Straneo 1967

I take this opportunity to complete the original description of this species, which lacked description of the underside because the lines of the manuscript on this subject were accidentally omitted: Underside entirely impunctate; proepisterna moderately shiny; metepisterna sericeous because of the strong microsculpture and twice as long as anterior width; abdominal sterna moderately shiny; last sternum with 1 + 1 (male) or 2 + 2 (female) setae.

The three known species of Group 16 are superficially similar, but easily distinguished by a number of characters. In the short description of *L. opaculus,* Bates did not specify the shape of the sides of the pronotum. But subsequently in description of *L. sculptilis* (Bates, 1884:278), he compared *L. sculptilis* Bates with *L. opaculus* Bates and wrote "*L. opaculus* differs conspicuously in the sides of the thorax being sinuated before the hind angles, and in the latter being slightly salient and rectangular as in *L. infimus.*" I have compared specimens of *L. sculptilis, L. infimus, L. negrei,* and *L. sericeus.* The South American *L. negrei* and *L. sericeus* are far more similar to *L. sculptilis* than to *L. opaculus.*

The three South American species may be determined by the following key:

1. Sides of pronotum subsinuate before slightly salient and rectangular hind angles (*teste* Bates); anterior submarginal border interrupted in middle; ventral surface clear ferrugineous red . *Loxandrus opaculus* Bates
1′. Sides of pronotum not sinuate before hind angles 2
2(1′). Sides of pronotum nearly uniformly rounded for entire length; hind angles rounded or blunt; pronotal base slightly wider than apex; anterior submarginal border entire .... *Loxandrus negrei* Straneo
2′. Sides of pronotum nearly straight and convergent toward base; base evidently wider than apex; hind angles nearly 90°; anterior submarginal border interrupted in middle .... *Loxandrus sericeus* Straneo

GROUP 17

Characters of the group.—Base of pronotum not bordered at sides; hind angles of pronotum markedly raised, with basal impressions very deep and wide cavities.

Described species.—*L. anchomenoides* Straneo and *L. attenuatus* Bates. This small group, which is a taxonomic unit probably worthy of subgeneric rank, includes two previously described species and two new ones. They may be determined by the following key.

1. Antennae normal, thin and moderately elongate; elytra with round sutural preapical red patch 2
1′. Antennae markedly thickened; elytra with or without sutural preapical red patch 3
2(1). Pronotum elongate (Fig. 67) ....*Loxandrus attenuatus* Bates
2′. Pronotum transverse (Fig. 66a) .....*Loxandrus reflexicollis,* new species
3(1′). Elytra without red patch; size larger (8.7 mm); legs concolorous .... *Loxandrus anchomenoides* Straneo
3′. Elytra with round preapical red patch; size smaller (7.8 mm); legs very pale yellow with dark knees ....*Loxandrus ornatellus,* new species

Loxandrus attenuatus Bates
(Fig. 67)

I identified as *L. attenuatus* Bates a specimen from Corumba, Brazil, in the collection of CMNH (Acc. No. 2966). It agrees with the description except in its size, which is nearly 1 mm larger, but the other characters (pronotum elongate, shape of lateral border and of basal foveae and angles, punctation of base and striae) are so distinctive that I have no doubt about the identity of this specimen. The species seems to be very rare, as this is the only specimen I have seen. The sketch of the pronotum (Fig. 67) was made from this specimen.

Loxandrus reflexicollis, new species
(Fig. 66a, b)

Type specimen.—Holotype, male (CS): Brasil, Jatahy [probably Jataí, Goias State]. Specimens examined: 1.

Diagnosis.—Group 17 species characterized by antennae thin and elongate (not greatly thickened), and pronotum transverse.

Description.—Length 6 mm; greatest width 2.4 mm. Head black; pronotum dark brown with lateral border slightly paler; elytra dark brown with lateral and apical border paler and with round, clearly defined red sutural anteapical patch on intervals 1–3 connected with apical margin along interval 1; underside brown; last sternum partly ferrugineous; legs, mouth, palpi and antennomeres 1–3 ferrugineous yellow, antennomeres 4–11 brown.

Head as long (1.2 mm) as wide (including eyes); eyes moderately large, convex; frontal impressions small, round, moderately deep; temples very short; front between eyes very convex; microsculpture indistinct at 35×.

Pronotum (Fig. 66a); length 1.4 mm; lateral border markedly widened posteriorly and markedly reflexed at basal angles; median longitudinal line deep and wide; microsculpture indistinct at 35×.

Elytra oval, disc slightly convex; length 3.4 mm, greatest width 2.4 mm; humeri very obtusely rounded; basal border joined to lateral margin without angle; sides behind posthumeral curve moderately and uniformly rounded; greatest width at midlength; preapical sinuosity moderate; striae deep, densely punctulate on disc; intervals moderately convex; puncture of interval 3 very small, at about midlength; microsculpture indistinct at 35×.

Legs slender; tarsomeres 5 with few very thin setae ventrally; hind tarsomeres not carinate dorsally; hind tarsomere 1 as long as 5 and as long as 2 + 3.

Underside impunctate, shiny; metepisterna very much narrowed posteriorly, nearly 1.75 times as long as anterior width.

Aedeagus as in Fig. 66b.

Remarks.—In the collections of CMNH is a specimen labelled: "Chapada, Brazil, Acc. 2966" and with two other labels, "Chapada Forest Stream" and "June." This has all the characters of *L. reflexicollis* but is larger (7 mm) and has antennomeres 3–11 dark brown. I labelled it ?*Loxandrus reflexicollis,* new species, but did not include it as a paratype.

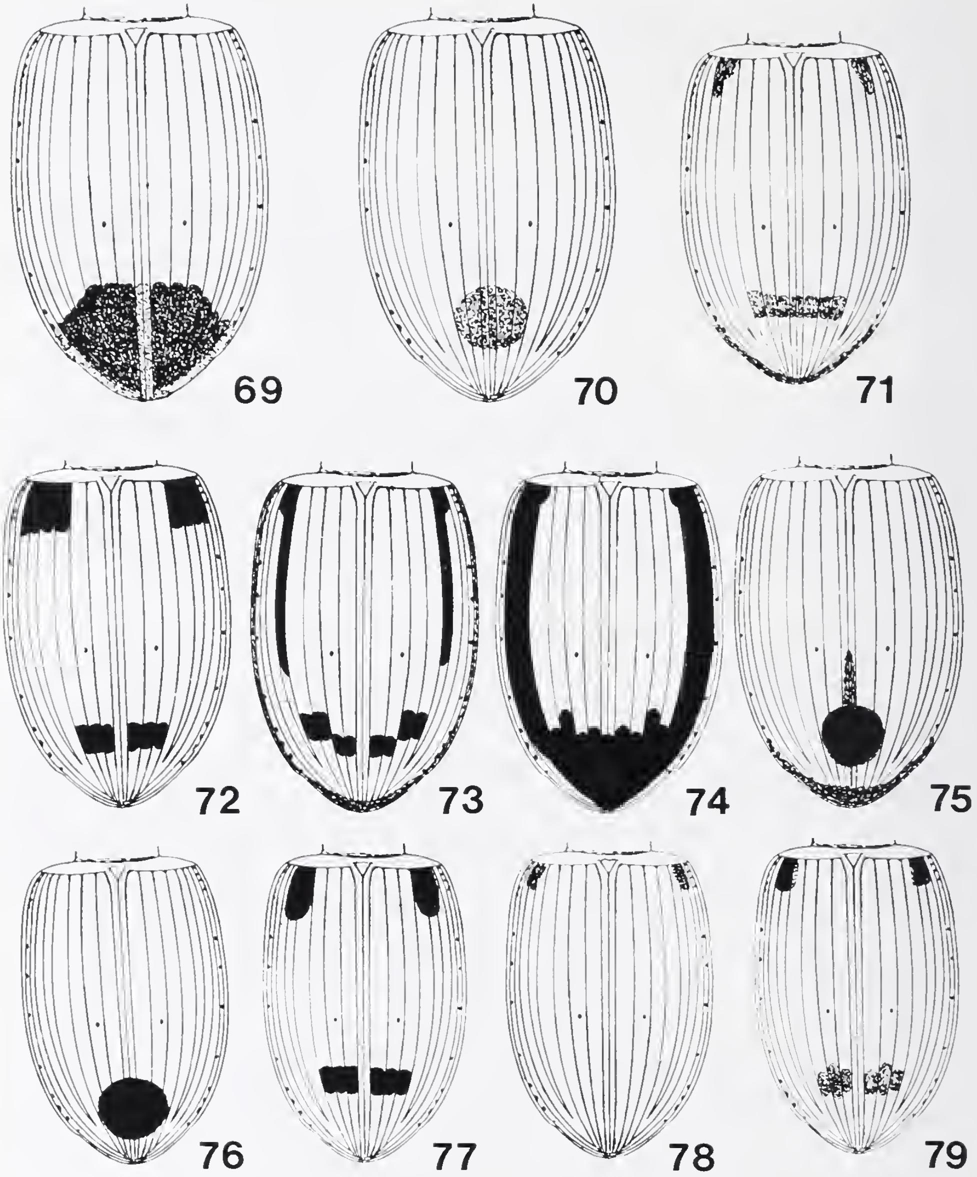

Fig. 69–79.—Schema of the patterns on elytra of South American *Loxandrus*. The figures indicated with f.d. are drawn from description. 69. *L. rubroniger*, new species. 70. *L. kayae*, new species. 71. *L. ornatus* Putzeys (f.d.). 72. *L. quadrinotatus* Bates (f.d.). 73. *L. vittatus* Bates (f.d.). 74. *L. fasciatus* Tschitschérine. 75. *L. trapezicollis*, new species. 76. *L. kochalkai*, new species. 77. *L. maculatus* Straneo. 78. *L. ecuadoricus*, new species. 79. *L. cribratellus*, new species.

Loxandrus ornatellus, new species
(Fig. 68a, b)

Type specimen.—Holotype, male (CS): Parq. Nac. Cerro Cord. Dpto Amambay Paraguay 8.VI.1962 H. Ferreira coll. Specimens examined: 1.

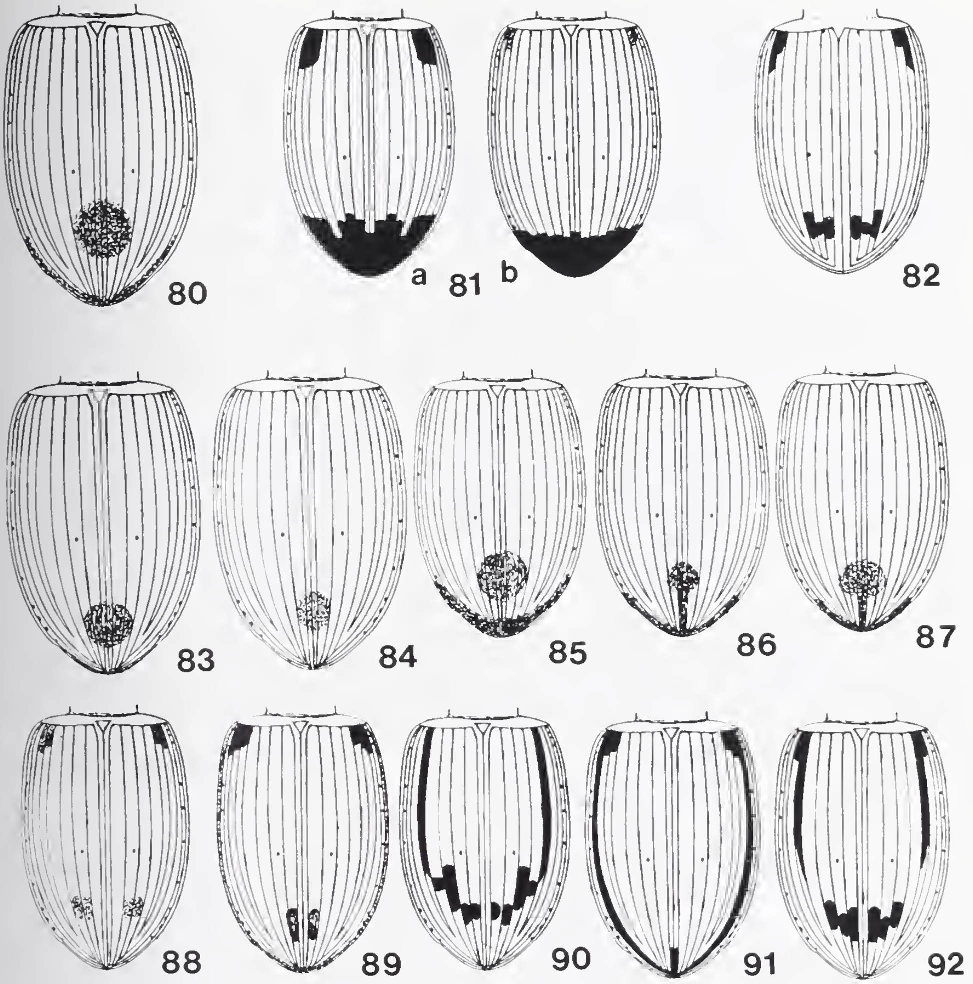

Fig. 80–92.—Schema of the patterns on elytra of South American *Loxandrus*. The figures indicated with f.d. are drawn from description. 80. *L. rufostigma* Bates (f.d.). 81a, b. *L. nicki* Straneo. 82. *L. humeralis,* new species. 83. *L. planoculis,* new species. 84. *L. posticus* Brullé (f.d.). 85. *L. guttula* Tschitschérine (f.d.). 86. *L. rubromaculatus* Straneo. 87. *L. davidsoni,* new species. 88. *L. pictoides,* new species. 89. *L. pictus* Tschitschérine. 90. *L. janeiranus,* new species. 91. *L. flavicauda* Tschitschérine. 92. *L. minasianus,* new species.

Diagnosis.—Group 17 species with markedly thickened antennae, legs yellow with dark knees, and elytra with round preapical red patch.

Description.—I limit the description to the characters not evident in the habitus (Fig. 68a). Length 7.8 mm; greatest width 2.6 mm. Upper surface black, shiny; elytra with red sutural anteapical patch and reddish apex; femora and tibiae pale yellow with darkened knees; tarsomeres brown; antennomere 1 ferrugineous, 2 and 3 brown, antennomeres 4–11 black; palpi ferrugineous. Antennomeres 4–11 thick, much wider than usual in *Loxandrus.* Tarsomeres 5 with few setae ventrally. Underside shiny; proepisterna smooth; mesosternum with many coarse punctures; metepisterna not sulcate along anterior and exterior sides, short, nearly as long as anterior width, with 5–9 coarse punctures; angles of metasternum with 3–4 punctures; last sternum with 1 + 1 (male) setae. Aedeagus with median lobe as in Fig. 68b.

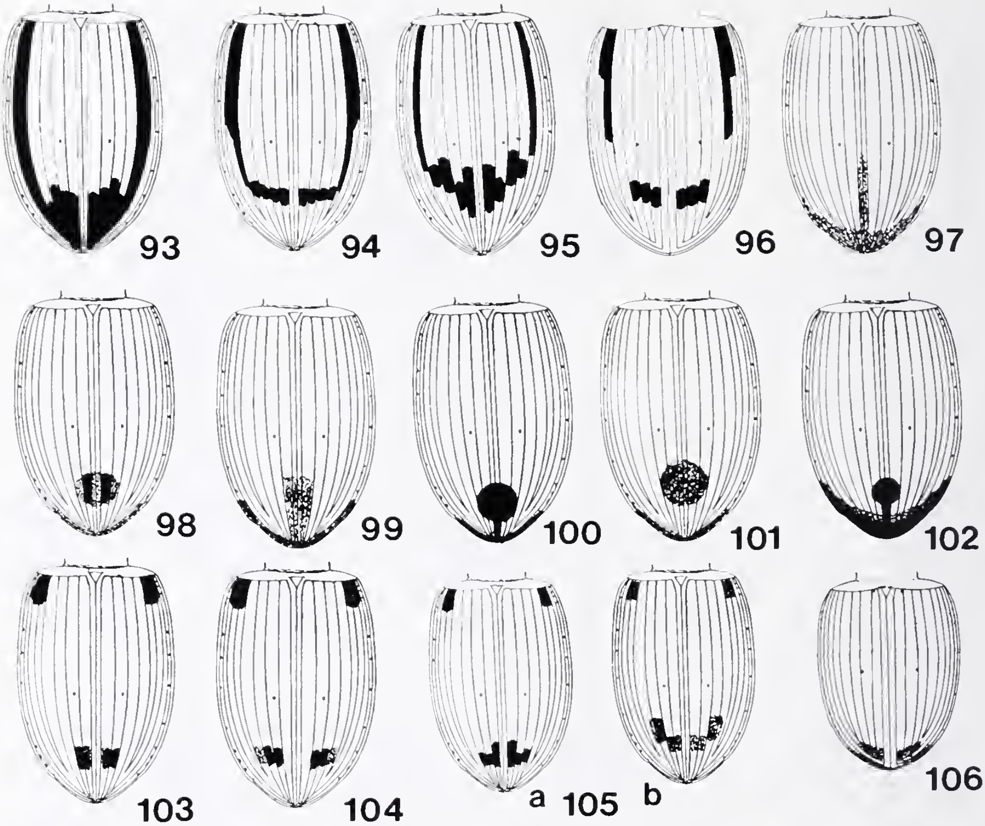

Fig. 93–106.—Schema of the patterns on elytra of South American *Loxandrus.* The figures indicated with f.d. are drawn from description. 93. *L. latifascia,* new species. 94. *L. fasciolatus* Tschitschérine (f.d.). 95. *L. subvittatus* Straneo. 96. *L. interruptus* Tschitschérine. 97. *L. sinuatellus,* new species. 98. *L. notula* Tschitschérine (f.d.). 99. *L. elaphropus* Tschitschérine. 100. *L. macula,* new species. 101. *L. photophilus,* new species. 102. *L. picticauda* Bates. 103. *L. similis,* new species. 104. *L. tetrastigma* Bates. 105a, b. *L. variabilis,* new species. 106. *L. brevis,* new species.

Species *incertae sedis*

Among the already known species listed with the groups, *Loxandrus idiocentrus* Tschitschérine is lacking because the description does not mention the submarginal border of the pronotum. As the base of the pronotum is not punctate and its sides are rounded, this species could belong to Group 1 or Group 2. However, if it is confirmed that the exceptional character of the apical spur of the protibia being dilated at the base is truly a species character and not an individual aberration, this species could require a group of its own. A second species, *Loxandrus confusus* Dejean, is lacking in the lists of described species because I did not recently see the type and I am not sure the specimen labelled "*confusus* Dej." in my collection is correctly determined. From the description, the sides of the pronotum are slightly subsinuate and the base is impunctate, so it may belong to Group 5 or Group 6 depending on the shape of the submarginal border.

ACKNOWLEDGMENTS

I thank sincerely Prof. G. E. Ball, University of Alberta, Robert L. Davidson, The Carnegie Museum of Natural History, Dr. F. Hieke, Museum für Naturkunde of the Humboldt University, Berlin, and the authorities of the Fundación Miguel Lillo, Tucumán, for the loan of the extremely interesting material that is the subject of this paper. I thank my friend, the late Jacques Nègre, for the donation of many fine *Loxandrus*. Moreover I am particularly grateful to Robert L. Davidson, John E. Rawlins and C. J. McCoy, who very kindly revised my manuscript.

Finally, I must point out that this paper would have been impossible without the help of Mr. Ph. Bruneau de Miré, Museum of Paris. He, with great patience and employment of time, checked, at my request, the characters omitted by Bates in his short descriptions of his South American *Loxandrus* (characters such as the anterior submarginal border of the pronotum, features of tarsi, etc., which were essential for identification of the species). I thank him sincerely.

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ANNALS OF CARNEGIE MUSEUM

Vol. 60, Number 1, Pp. 63–82 27 February 1991

REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 11. PALAEANODONTA (MAMMALIA)

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Abstract

New fossils of Palaeanodonta from the Wind River Formation (Wasatchian to earliest Bridgerian) of the Wind River Basin include at least four and possibly more species: the metacheiromyid cf. *Palaeanodon* sp. (possibly more than one species), the epoicotheriids *Pentapassalus woodi* and *Tubulodon taylori* (probably congeneric), and a new genus and species, *Dipassalus oryctes.* The latter is a diminutive, highly fossorial species with a reduced dentition resembling that of *Metacheiromys* (i.e., retention of only two vestigial postcanines) but with postcranial modifications foreshadowing those of the advanced Oligocene epoicotheriid *Epoicotherium.* The reduced dental condition is considered convergent, and *Dipassalus* is tentatively included in the Epoicotheriidae.

Introduction

The Palaeanodonta is a group of small, early Tertiary fossorially adapted mammals usually allied evolutionarily with the Pholidota and/or the Edentata (Xenarthra). Two families are recognized, Metacheiromyidae and Epoicotheriidae. In metacheiromyids the skull is generally somewhat longer, postcanine teeth are reduced to single-rooted pegs, and the posterior part of the dentary (and maxilla) is edentulous and marked by a distinct, dorsally rugose posteromedial shelf ("medial buttress"). Epoicotheriids generally have shorter skulls with teeth present to the back of the jaws (hence the medial buttress is less conspicuous), and they tend to be more specialized postcranially.

Palaeanodonts were first reported from the Wind River Basin by Matthew (1918:641–642, fig. 58–60), who considered these specimens—metacarpals and manual phalanges and an astragalus from the Lost Cabin beds—to represent two or more species "intermediate between *Palaeanodon* and *Metacheiromys* in specialization". His assessment was reasonable at the time, given that these metacheiromyids were the only two palaeanodont genera then known; however, at least some of the metacarpals are relatively shorter and more robust than in those genera and probably belong to an epoicotheriid close to the Lysitean species *Pentapassalus woodi.*

Jepsen (1932) described *Tubulodon taylori* from the upper part of the Wind

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Submitted 17 May 1990.

River Formation (Lost Cabin Member) based on dentary fragments of one individual. Citing several characters, including the presence of dentinal tubules, he allocated the taxon to Tubulidentata. Colbert (1941) rejected this assignment, questioning the homology of these tubules with those in *Orycteropus.* Without so stating, Gazin (1952) apparently considered *Tubulodon* to be an epoicotheriid, as did Simpson (1959) and subsequent authors explicitly.

Nearly half a century later, Guthrie (1967) described *Palaeanodon woodi,* based on a fragmentary skull, jaws, and partial skeleton from the Lysite Member. This species was later shown to be an epoicotheriid referable to the genus *Pentapassalus* (Rose, 1978).

No other palaeanodonts have been described from the Wind River Basin, although Stucky (1984) reported *Tubulodon* from the *Lambdotherium* Range Zone and the *Palaeosyops borealis* Assemblage Zone of the Wind River Formation (Lostcabinian and Gardnerbuttean respectively; Krishtalka *et al.,* 1987). The type specimen of *Tubulodon taylori* was recovered from rocks now known to be of Gardnerbuttean age.

New materials collected from Lysitean, Lostcabinian, and Gardnerbuttean horizons (later Wasatchian through earliest Bridgerian) in the Wind River Formation in recent years by field parties from The Carnegie Museum of Natural History considerably expand our knowledge of Wind River Basin palaeanodonts. At least three and possibly four genera are represented: the metacheiromyid *Palaeanodon,* the epoicotheriids *Tubulodon* and *Pentapassalus* (probably congeneric), and a specialized new genus probably referable to the Epoicotheriidae. These new specimens add to increasing evidence that palaeanodonts were both more common and more diversified, and their phylogeny considerably more complex, than previously believed.

Abbreviations are as follows: AC, Pratt Museum, Amherst College, Amherst; AMNH, American Museum of Natural History, New York; CM, The Carnegie Museum of Natural History, Pittsburgh; PU, Princeton University collection at Yale Peabody Museum, New Haven; UCM, University of Colorado Museum, Boulder; UM, University of Michigan Museum of Paleontology, Ann Arbor; USGS, Paleontology and Stratigraphy Branch, U.S. Geological Survey, Denver; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATIC PALEONTOLOGY

Order Uncertain
Suborder Palaeanodonta Matthew, 1918
Family Metacheiromyidae Wortman, 1903
Palaeanodon Matthew, 1918
cf. *Palaeanodon* sp.
(Fig. 1)

Referred specimens.—CM 43752, posterior part of left dentary; CM 47159, posterior part of left dentary.

Localities.—CM locs. 937, 1040 (Lostcabinian, Lost Cabin Member).

Discussion.—The two specimens reported here, both posterior halves of left dentaries, are similar to *Palaeanodon* and are closest in overall size and in size of postcanine alveoli to early Wasatchian *P. ignavus* Matthew, the largest species of the genus. Only two other species of the genus have been named, and both are

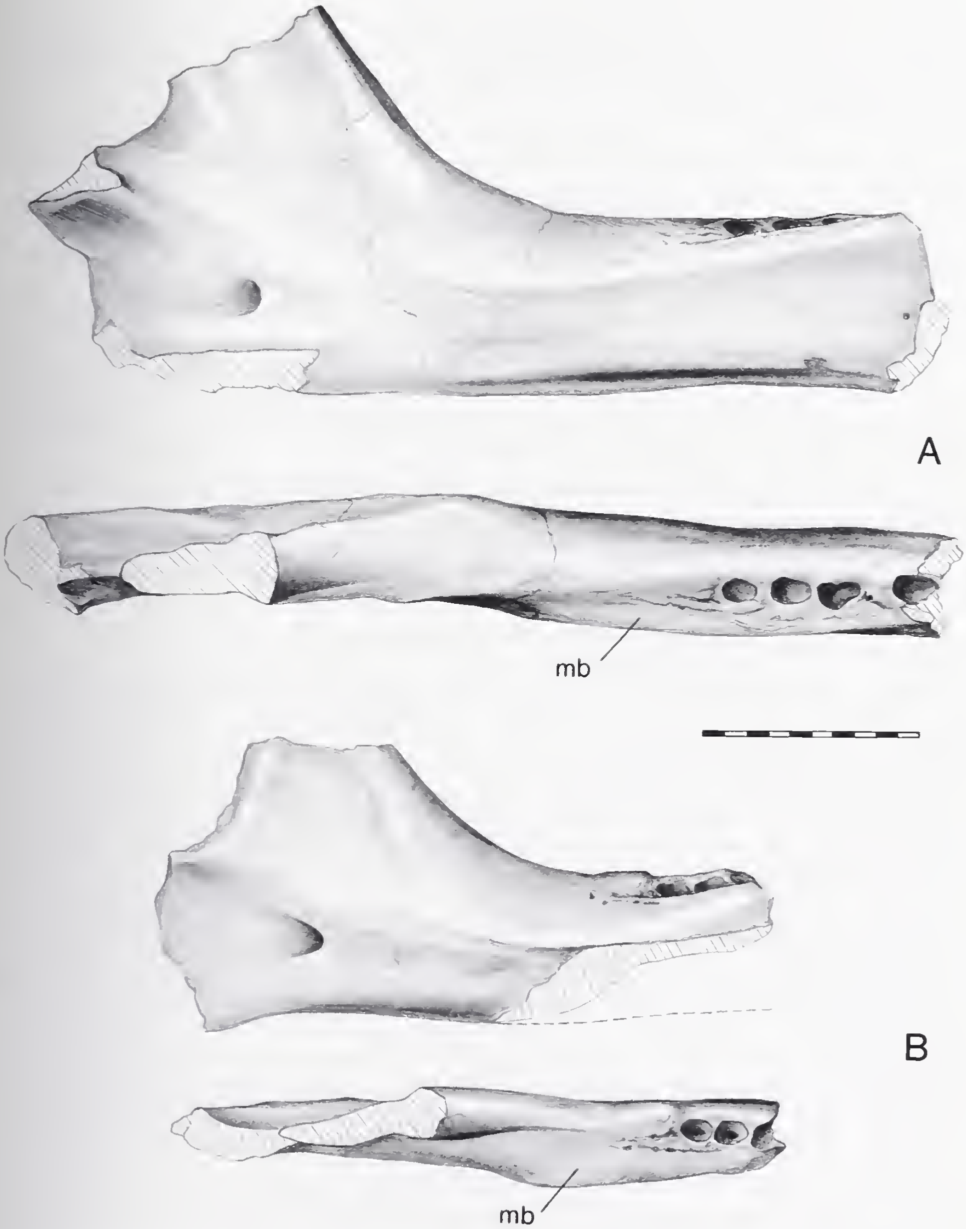


Fig. 1.—Left dentary fragments of cf. *Palaeanodon* species. (A) CM 47159; (B) CM 43752. Scale is 10 mm; mb indicates medial buttress.

smaller and known only from older beds: *P. parvulus* Matthew, 1918 (Clarkforkian), and *P. nievelti* Gingerich, 1989 (earliest Wasatchian). It has been clear for some time that the taxonomy of *Palaeanodon* was more complex than indicated by these few species; but a better understanding of the genus is hampered by the paucity of good specimens, uncertainty as to the extent of sexual dimorphism or other intraspecific variation (for instance, in size, jaw depth, or robustness), and uncertainty over the taxonomic significance of differences in conformation of the postcanine teeth. A systematic revision may soon be worthwhile but is beyond the scope of this report.

It is notable that the two dentary fragments (Fig. 1) differ markedly in robustness and in size and spacing of the teeth. CM 43752 is smaller and more gracile, with two diminutive, closely approximated alveoli for posterior postcanines. (The form and complete number of postcanines is unknown; in Bighorn Basin *Palaeanodon ignavus* there are five single-rooted peglike postcanines.) CM 47159 is more robust and preserves four somewhat larger postcanine alveoli. The anteriormost, broken in front, is larger than the three behind (which are closely spaced) and is separated from them by a short diastema. The next one (the most anterior complete alveolus), is faintly constricted anteriorly, suggesting a bilobed root (as in some specimens of *Palaeanodon ignavus,* e.g., USGS 21876, as well as the more primitive *Propalaeanodon* and epoicotheriids). Both specimens exhibit an edentulous posteromedial shelf ("medial buttress"), but it is less prominent than in *P. ignavus* and does not extend posteriorly below the coronoid process as in that species. Whether these differences can be ascribed to intraspecific variation (including sexual dimorphism) or to specific distinction is conjectural; therefore, the specimens are here assigned to cf. *Palaeanodon* species.

Family Epoicotheriidae Simpson, 1927

Three genera of Wasatchian epoicotheriids have been named: *Pentapassalus* [two species, *P. pearcei* Gazin and *P. woodi* (Guthrie)] and the monotypic genera *Tubulodon* (*T. taylori* Jepsen) and *Alocodontulum* (*A. atopum* Rose, Bown, and Simons). Each species was based on a single individual, and only two Wasatchian epoicotheriid specimens besides the holotypes have been reported (Guthrie, 1971; Rose, 1990). *Pentapassalus pearcei* was founded on a complete skull and partial skeleton; *P. woodi* on a rostrum, dentaries, and partial skeleton that are less well preserved than the holotype of *P. pearcei*; *Tubulodon taylori* on fragmentary dentaries; and *Alocodontulum atopum* on a maxilla and poorly preserved associated fragments. The latter two species are dentally similar but not directly comparable, and the teeth in both are less heavily worn than in the two specimens of *Pentapassalus,* making comparisons difficult. Thus, the principal differences between these taxa now seem to relate to degree of tooth wear and the fact that the holotype of *T. taylori* is a lower dentition whereas that of *A. atopum* is an upper dentition. The new specimens described below, together with other new material under study by R. J. Emry and Rose, show stages of tooth wear that bridge the morphologic gaps between these taxa and suggest that all four species are congeneric (in which case the proper name is *Tubulodon*). However, putative discrepancies between them in tooth number and root configuration of P_4–M_2, as well as size, are not resolved. Pending further study, they are here described under the existing names.

Pentapassalus Gazin, 1952

Pentapassalus woodi (Guthrie, 1967)

Referred specimens.—CM 45150, partial skeleton including posterior part of left dentary, numerous vertebrae, ribs, and sternebrae, incomplete left humerus, ulnae, distal radii, partial innominate, left femur, proximal and distal tibia, patella, and a few metapodials and phalanges; and questionably CM 43750, right metacarpal III, and CM 22307, right astragalus.

Table 1.—*Dimensions (mm) of the astragalus of some palaeanodonts. Abbreviations: B, breadth; e, estimated; H, dorsoplantar height; L, proximodistal length, from trochlear groove; Troch, trochlea.*

Taxon, specimen no.	Troch B	Troch L	Troch B/L	Astrag L	Head B	Head H	Head H/B
Dipassalus oryctes, CM 43286 (holotype)	2.7	2.0e	1.35	3.9	1.9	1.3	0.68
Palaeanodon ignavus, USGS 16471	8.1	7.1	1.13	12.4	6.6	4.5	0.68
?*Alocodontulum atopum*, USGS 3933	8.0	5.3e	1.51	9.4	5.0	3.3	0.66
Pentapassalus woodi, AC 2766 (holotype)	7.9	5.4	1.46	10.1	5.4	3.8	0.70
?*Pentapassalus* sp., CM 22307	10.9	6.5	1.68	11.6	6.4	4.0	0.63

Localities.—CM locs. 90, 1077 (Lostcabinian), 34 (Gardnerbuttean), all Lost Cabin Member.

Discussion.—The partial skeleton (CM 45150) is closely comparable to the holotype skeleton (AC 2766) but slightly smaller. In fact, apart from the trivial size difference and a stronger teres tubercle on the humerus of CM 45150, no significant difference from the type specimen was detected in any element. Although it does not add significantly to our knowledge based on the holotype skeleton, this specimen is important in confirming the morphology and size of the species. In the associated dentary fragment the last postcanine alveolus is situated just anterior to the coronoid process, as in *Pentapassalus,* but in contrast to *Palaeanodon* in which this part of the dentary is edentulous. The alveolus is relatively slightly anterior to the position of the last postcanine in *Tubulodon taylori,* but whether this difference is taxonomically significant is unknown. As in the holotype, the metacarpals are relatively shorter and more robust than in *Palaeanodon.*

CM 43750, a third metacarpal, is slightly smaller than in the holotype of *P. woodi* and almost exactly the size of this element in *P. pearcei*; however, the two species differ little in size of metapodials. It has similar proportions to the third metacarpal in both species of *Pentapassalus* and is relatively shorter than in *Palaeanodon ignavus.*

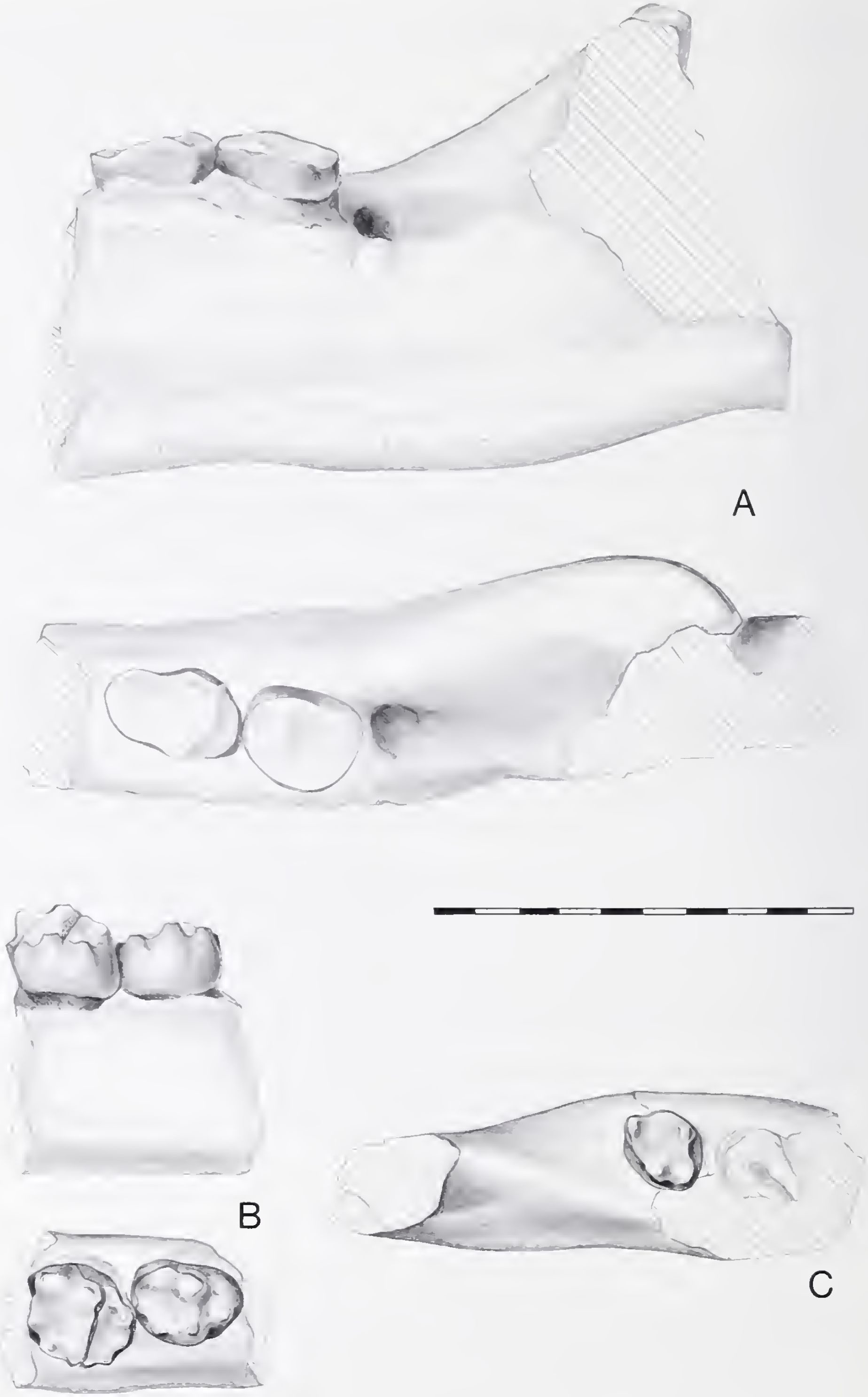
CM 22307 is an astragalus of a large palaeanodont, possibly this species. It is distinctive in having a very wide body, dorsoventrally compressed but with a well-excavated trochlea, and a short, broad, and flattened neck and head. In all these traits it more closely approaches the astragalus of *Pentapassalus* than *Palaeanodon* (*contra* Guthrie, 1971; however, transfer of Guthrie's *Palaeanodon woodi* to *Pentapassalus* did not come until later) and, therefore, probably represents an epoicotheriid. It is, however, larger and relatively broader than in the holotype of *Pentapassalus woodi* (Table 1), and its assignment here is tentative.

Tubulodon Jepsen, 1932
Tubulodon taylori Jepsen, 1932
(Fig. 2)

Referred specimens.—CM 22302, right dentary with M$_3$; CM 34854, left dentary with M$_{1-2}$, three associated vertebrae (thoracic?) and fragmentary astragalus; and tentatively CM 36939, right dentary with M$_{1-2}$, and CM 39682, left dentary with ?M$_1$.

Localities.—CM loc. 803 (Lysitean, Lysite Member), CM loc. 1549 (Lostcabinian, Lost Cabin Member), CM loc. 34 (Gardnerbuttean, Lost Cabin Member).

Discussion.—Since Jepsen's description of the holotype dentaries only one additional specimen has been referred to this species, CM 22302, a dentary with


A
B
C

M_3 (Fig. 2C; see also Guthrie, 1971). The long axis of the tooth is transversely oriented, suggesting that it was dislodged and rotated before fossilization. Cusp homologies are unclear, even compared to M_{1-2} in the holotype; nonetheless, the size and morphology closely approximate those of the holotype. In addition, the tooth is situated just anterior to the base of the coronoid process, as in the type specimen of *Tubulodon taylori,* and relatively a little more posterior than in *Pentapassalus woodi.*

A second specimen, a dentary fragment with M_{1-2} (CM 34854), certainly represents *Tubulodon taylori,* as it closely resembles the type specimen in size and morphology (Fig. 2B). Cusp homologies are ambiguous, particularly on M_2, but standard cusps may be tentatively recognized on M_1 and, except for the presence of a probable hypoconulid (not discernable in the holotype), agree with Jepsen's description. Thin enamel surrounds each tooth but, even in this minimally worn specimen, no enamel can be detected on the occlusal surface. The roots appear single at the base of the crown, although that of M_1 is faintly bilobate.

Two other specimens closely resemble *Tubulodon taylori* despite minor differences. CM 36939 is a robust dentary fragment containing two comparatively large teeth (M_{1-2}) worn almost flat (Fig. 2A); the minimal relief left suggests that a less worn state would resemble the holotype of *T. taylori.* Thin enamel surrounds each tooth but is absent from the occlusal surface. The teeth are closely appressed (without intervening diastemata), as in the holotype, but a little larger, and the alveolus for M_3 is posteriorly situated. CM 39682 contains a single cheek tooth (molar?) with two prominent peripheral cusps, perhaps a protoconid and metaconid; the remaining cusps are nearly obliterated by wear. Although the dentary is conspicuously more robust than in the holotype, the tooth is the same size as in the type specimen and the original crown anatomy appears to have been the same.

?Epoicotheriidae

Dipassalus, new genus

Type and only known species.—D. oryctes, new species.

Diagnosis.—Small palaeanodont about the size of *Epoicotherium unicum* and with relatively short jaws. Differs from all other palaeanodonts except *Metacheiromys* in having only two single-rooted, peglike postcanines in each jaw, upper and lower; posterior half of dentary edentulous and with well-developed medial buttress. Humerus with elongate, straight deltopectoral crest, pectoral process not as well defined or as elevated as in other species, prominent laterally projecting deltoid process, head proximodistally elongate, and lesser tuberosity projecting mediodistad more than in *Pentapassalus* but less than in *Epoicotherium* (all features in contrast with *Metacheiromys*).

Etymology.—Greek, *di,* two, and *passalus,* peg, in allusion to the two peglike postcanine teeth in each maxilla and dentary.

←

Fig. 2.—Dentary fragments of *Tubulodon taylori.* (A) CM 36939, right dentary with M_{1-2} and alveolus of M_3 in medial and dorsal views, tentatively assigned to *T. taylori*; (B) CM 34854, left dentary with M_{1-2} in medial and dorsal views; (C) CM 22302, right dentary with M_3 in dorsal view. Scale is 10 mm.

Dipassalus oryctes, new species
(Fig. 3–5, 8, 9)

Holotype.—CM 43286, partial skeleton including left and right maxillae occluded with dentaries, fragmentary left scapula, right humerus, right pelvis, left femur, proximal and distal right femur, proximal and distal right tibia and fibula, right astragalus, and a few associated vertebrae; found by Susan Rose.

Type locality.—CM loc. 34 (Gardnerbuttean, Lost Cabin Member), Wind River Basin, Wyoming.

Referred specimens.—CM 34736, 43282, 43284, 43747, 43748, 43749, 47195, and UCM 45317 (all proximal humeri), CM 43283 (posterior left dentary), CM 43287 (proximal humerus and cervical vertebrae in nodule) and, tentatively, CM 43751 (proximal left humerus).

Localities.—CM locs. 807 (Lysitean, Lysite Member), 91, 858, 1036, 1040 (all Lostcabinian, Lost Cabin Member), 34 (Gardnerbuttean, Lost Cabin Member).

Known distribution.—Middle Wasatchian through earliest Bridgerian (Lysitean through Gardnerbuttean)—Wind River Basin (Wind River Formation), Wyoming.

Etymology.—Greek *oryctes,* digger.

Diagnosis.—As for genus.

Description and comparison.—**Cranium and Dentaries:** The cranial fragments included with the holotype are poorly preserved but clearly belong to a small palaeanodont, as indicated by the characteristic robust canines (the upper canine honed flat on its anterior surface by the lower canine, the lower honed flat posteriorly), reduced number of degenerate cheek teeth, and distinctive medial buttress of the dentary (Fig. 3). Similarly, many of the postcranial elements bear unmistakable hallmarks of the Palaeanodonta. The following description pertains to the holotype except where otherwise indicated.

Both the maxilla and the dentary apparently hold two one-rooted, peglike postcanine teeth behind the large canines, but, owing to the poor state of preservation, the number of postcanines is not absolutely certain. On the left side (Fig. 3A), for example, a small tooth chip situated immediately behind the canine root appears at first glance to be a lower postcanine (in which case there would be three). On closer inspection, however, the chip seems to be affixed to the lateral side of the dentary near the root of the canine, and to match a broken edge on the tip of the upper canine. If added to the upper left canine as preserved, the total length closely approximates that of the complete upper right canine. Further preparation that might clarify the situation was deemed too risky to the specimen (the surface of the bone is softer than the matrix and in many places difficult to distinguish from it). The right dentary seems to possess only two postcanines; a tooth believed to be the first postcanine was dislodged from its alveolus and now lies deep to the upper canine (Fig. 3B). Glimpses of two upper postcanines are visible through hard matrix on the left side; only the second is in place on the right. Poor preservation of the teeth makes it difficult to ascertain if enamel was present; if so, it was very thin.

All palaeanodonts in which the anterior part of the dentary is known possess one incisor in a shallow spoutlike projection of the dentary. In the absence of this part of the jaw in any specimen of *Dipassalus,* presence of this tooth is conjectural. However, the configuration of the bone surrounding the canine root, though broken, suggests the possibility that the dentary ends at the canine, without the spoutlike projection.

Behind the two postcanines in each jaw is a short edentulous portion. In the dentary this is distinguished by a medially projecting shelf ("medial buttress"), roughened on its dorsal surface, that inclines ventromediad as it approaches the coronoid process. It occurs in the holotype but is better preserved (and perhaps more strongly developed) in CM 43283 where the posterior part of the dentary is more nearly complete (Fig. 4); the medial buttress in the latter specimen closely resembles that of *Palaeanodon.* Matthew (1918) and Simpson (1931) suggested that the medial buttress may have supported a corneous pad, as in *Ornithorhynchus.* In CM 43283 the angle of the dentary is sharply downturned and slightly inflected as in *Epoicotherium unicum* (Rose and Emry, 1983) and *Tetrapassalus mckennai* (Simpson, 1959), but the latter lacks a well-developed medial buttress. The coronoid process rises more steeply in CM 43283 than in *T. mckennai.* The mental foramen is situated below the second postcanine, as in *T. mckennai* and *E. unicum.* The complete dentary is restored in Fig. 3C.

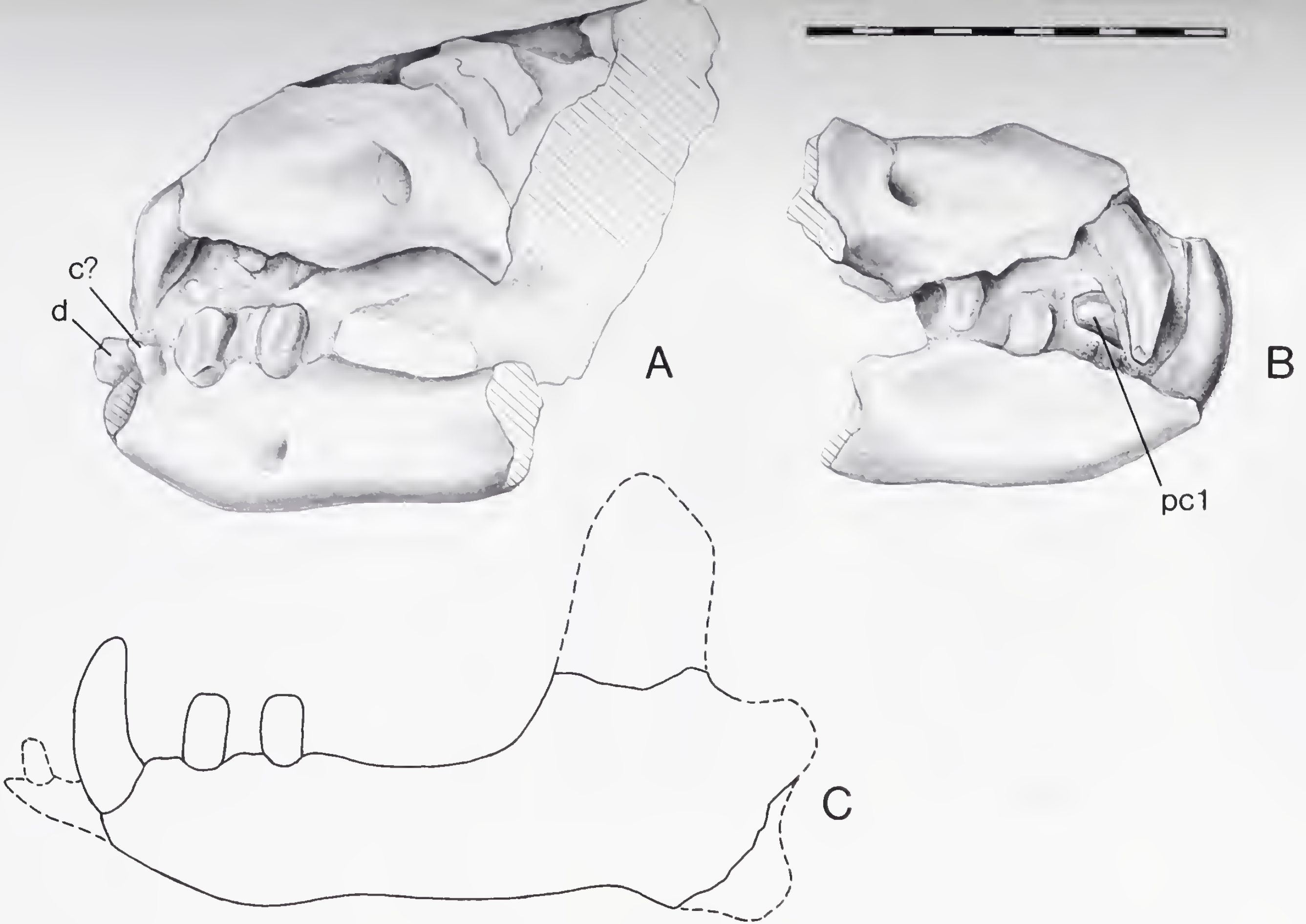


Fig. 3.—*Dipassalus oryctes,* new genus and species, CM 43286 (holotype). (A) Left side of rostrum with the canine and two postcanines partially visible through matrix, and left dentary with canine root and two postcanines. Abbreviations: c?—probable fragment of the upper canine, appressed against the lateral side of the dentary; d—medial side of dentary projecting in front of broken canine root. (B) Right side of rostrum and right dentary with canines and second postcanines; pc1 indicates probable first postcanine dislodged from its alveolus and protruding from matrix deep to the upper canine. (C) Restoration of dentary based on holotype and CM 43283. Scale is 10 mm.

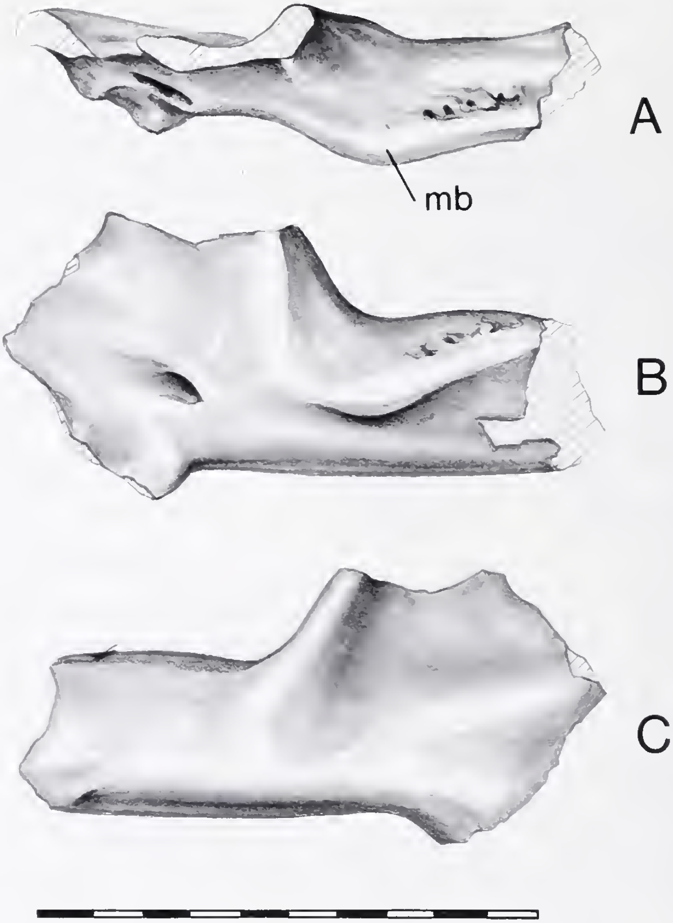


Fig. 4.—*Dipassalus oryctes*, new genus and species, CM 43283, posterior left dentary in (A) dorsal, (B) medial, and (C) lateral views; mb indicates medial buttress. Scale is 10 mm.

A large infraorbital foramen is present on the maxilla behind the second postcanine.

Vertebrae: The few fragmentary vertebrae associated with the type specimen are not particularly distinctive. More interesting, however, are eight articulated vertebrae preserved in a small nodule also containing a proximal humerus of *Dipassalus oryctes* (CM 43287). They are visible only in ventral view, but this is sufficient to indicate that they belong to the posterior cervical and anterior thoracic sequence of a small palaeanodont (probably the same individual as the humerus). The centra are very short and broad but there is no indication of cervical fusion, in contrast to the situation in *Epoicotherium* and *Xenocranium* (Rose and Emry, 1983). The series is bent sharply—slightly more than 90 degrees—near the apparent cervical-thoracic juncture and, consequently, is strongly concave dorsally. A very similar pronounced cervicothoracic flexure (lordosis) exists in dasypodids, partly facilitated by modifications in the seventh cervical. The prominent flexure in CM 43287 thus appears to have been the condition in life rather than a result of postmortem distortion and, in analogy with dasypodids, the flexure is presumed to occur at C7. On this basis the vertebrae are identified as C3–7 and T1–3.

An abrupt cervicothoracic lordosis also occurs in chrysochlorids and shrews and is expressed to extreme in *Scutisorex* (Kingdon, 1974). Kingdon suggested that in *Scutisorex* this flexure is associated with a change in posture and in orientation of the thorax, but he also observed that "more forceful movements of the shoulders and head were also employed to push into crevices and vegetable debris, . . . probably connected with feeding behaviour" (1974:90). In chrysochlorids, the flexure accommodates powerful neck and shoulder musculature associated with digging (Puttick and Jarvis, 1977), and it appears to be functionally related to use of the head to dig (Gasc *et al.*, 1986). The resemblance of the cervicothoracic vertebral series in CM 43287 to that in chrysochlorids and dasypodids is evidence of the fossorial behavior of *Dipassalus*; and it suggests that, like chrysochlorids (and as inferred for *Xenocranium* and *Epoicotherium*), *Dipassalus* actively used its head in digging.

Scapula: A fragment of the cranial end of the left scapula displays a shallow glenoid fossa and well-developed coracoid process. The spine is incomplete but enough is present to show that it was relatively low and directed ventrally over the infraspinous fossa, much as in *Epoicotherium unicum* and less like other palaeanodonts. The correspondence is not exact, however, and the element is too incomplete to provide much additional information.

Humerus: The humerus is the most distinctive postcranial element and is represented by several specimens (Fig. 5), all of which contribute to the following description. In overall proportions the humerus of *Dipassalus* is relatively broad and short, resembling in this regard that of *Epoicotherium* and an incomplete humerus (CM 62653; Fig. 6) from the Bridgerian of Utah (Powder Wash) identified here as ?*Tetrapassalus* sp. It is slightly longer than in *Epoicotherium* and ?*Tetrapassalus* but much smaller than in other palaeanodonts. The head is elliptical, approaching the shape in *Epoicotherium* and comparatively much narrower mediolaterally and more elongate proximodistally than in any other palaeanodont except ?*Tetrapassalus* sp. (Table 2).

The proximal extent of the greater tuberosity is typically about even with the humeral head and in some specimens projects proximal to the head (e.g., CM 43282, 43751). The latter condition is characteristic of most palaeanodonts, whereas in *Epoicotherium* (Fig. 6B) and *Xenocranium* the greater tuberosity is reduced and its proximal extent is below that of the head. The lesser tuberosity is prominent and projects medially much more so than in *Pentapassalus* (Fig. 7) or *Metacheiromys* but less than in *Epoicotherium* (where the lower end of the tuberosity may actually be continuous with the teres tubercle; Turnbull and Reed, 1967). The relative expression of these tuberosities closely approximates that in chrysochlorids, adept forelimb diggers in which the subscapularis (a medial rotator of the humerus that attaches to the lesser tuberosity) is particularly powerful, whereas supraspinatus and infraspinatus (lateral rotators inserting on the greater tuberosity) are reduced (Gasc *et al.*, 1986).

In *Dipassalus* the attachment of teres major is separate and indicated by a thickening of the medial border of the shaft at or just distal to midshaft. Most other palaeanodonts have a similar but somewhat more proximal teres tubercle, but in *Xenocranium* this tubercle, when present, is distal to midshaft (Rose and Emry, 1983). *Epoicotherium* lacks a teres tubercle (Turnbull and Reed, 1967; Rose and Emry, 1983).

The shaft is relatively broad and, as in *Epoicotherium*, not as deep anteroposteriorly as in other palaeanodonts, as a result of its less-elevated deltopectoral crest. The crest is elongate (extending four-fifths of humeral length; Table 2) and its medial border is straight, not arcuate as in ?*Tetrapassalus* and *Epoicotherium* (Fig. 6), nor does it overhang the bicipital groove as in those genera. It is shelflike and broad proximally, gradually tapering distally to a rounded point (presumably the pectoral process) as the pectoral crest converges with the deltoid crest. As in other palaeanodonts, this configuration indicates very distal insertions of pectoralis major and deltoideus, an adaptation to enhance powerful forelimb movements as in various other specialized diggers. Near the proximal end of the deltoid crest is a very prominent deltoid tubercle that projects laterad, proximal and anterior to the tip of the supinator crest. This tubercle is variable in form in the available specimens, ranging from spinelike to crestlike (Fig. 5). In contrast to all other palaeanodonts, the pectoral process is neither conspicuously elevated (as in metacheiromyids and *Pentapassalus*; e.g., Simpson, 1931; Gazin, 1952) nor knoblike (?*Tetrapassalus, Epoicotherium,* and *Xenocranium*; Fig. 6; Rose and Emry, 1983).

The bicipital groove is broader and less well defined than in other palaeanodonts, although proximally it is completely roofed by bone extending between the tuberosities, forming an osseous tunnel for the biceps tendon. A similar condition occurs in *Epoicotherium,* but in the latter the osseous tunnel is more distal and is formed by a bridge between the lower part of the lesser tuberosity and the upper part of the pectoral crest (compare Fig. 5A and 6B). Hence, formation of an osseous bicipital tunnel may have occurred in parallel in *Dipassalus* and *Epoicotherium.*

The distal end of the humerus is present only in the holotype, where it is incomplete. Preservation is adequate to show that the trochlea is very broad and shallow (approximately intermediate in form between *Pentapassalus pearcei* and *Epoicotherium unicum* (Fig. 6B, 7) and the capitulum is obliquely ovoid but approaching spherical. The medial epicondyle is broken away. As is typical in palaeanodonts, the supinator crest is exaggerated, flaring laterally and extending proximally about 50% of humeral length—relatively a little more than in *Metacheiromys* but less than in *P. pearcei* or *E. unicum* (Table 2). The proximal tip of the supinator crest is somewhat less hooklike than in the latter two species, more closely approximating that in ?*Tetrapassalus* (compare Fig. 5 and 6).

CM 43751, a proximal humerus from the Lysite Member (CM loc. 807, Lysitean) is older than the

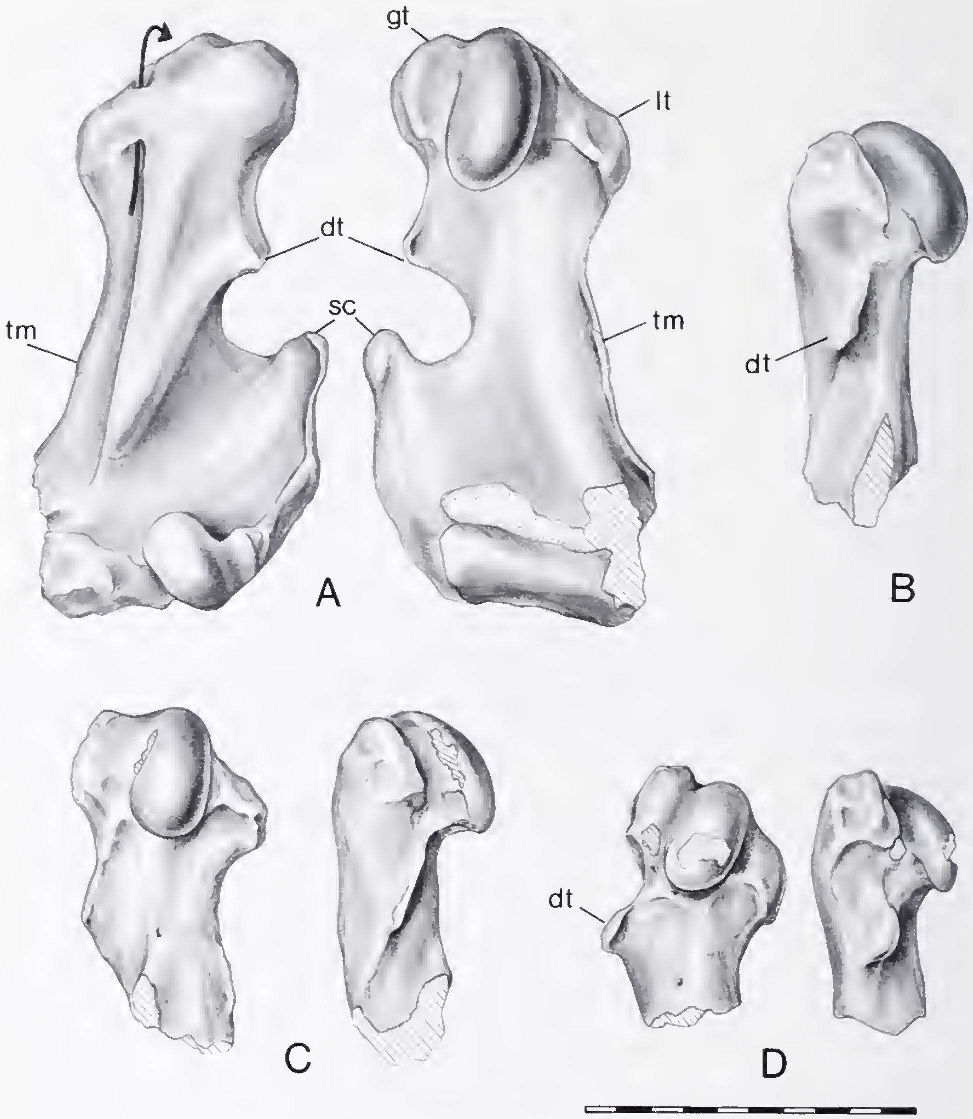


Fig. 5.—Humeri of *Dipassalus oryctes,* new genus and species. (A) CM 43286 (holotype), right humerus (reversed), with deltoid tubercle partly restored from CM 43747, in anterior and posterior views; (B) CM 43747, proximal right humerus (reversed) in lateral view; (C) CM 43282, proximal left humerus in posterior and lateral views; (D) CM 43751, proximal left humerus in posterior and lateral views. Abbreviations: dt—deltoid tubercle; gt—greater tuberosity; lt—lesser tuberosity; sc—supinator crest; tm—tubercle for insertion of teres major. Scale is 10 mm.

remainder of the sample (Lostcabinian and Gardnerbuttean) and differs from the others in several characters (Fig. 5D). The greater tuberosity projects noticeably proximal to the head, the lesser tuberosity extends slightly less medially, and the bicipital groove is well defined but not enclosed in an osseous tunnel. In addition, the deltoid tubercle forms a salient, rounded process, less crestlike or elongate than in other specimens. These presumably more primitive characters may be taxonomically significant, but in the absence of any other specimens, CM 43751 is tentatively included with *Dipassalus oryctes.*

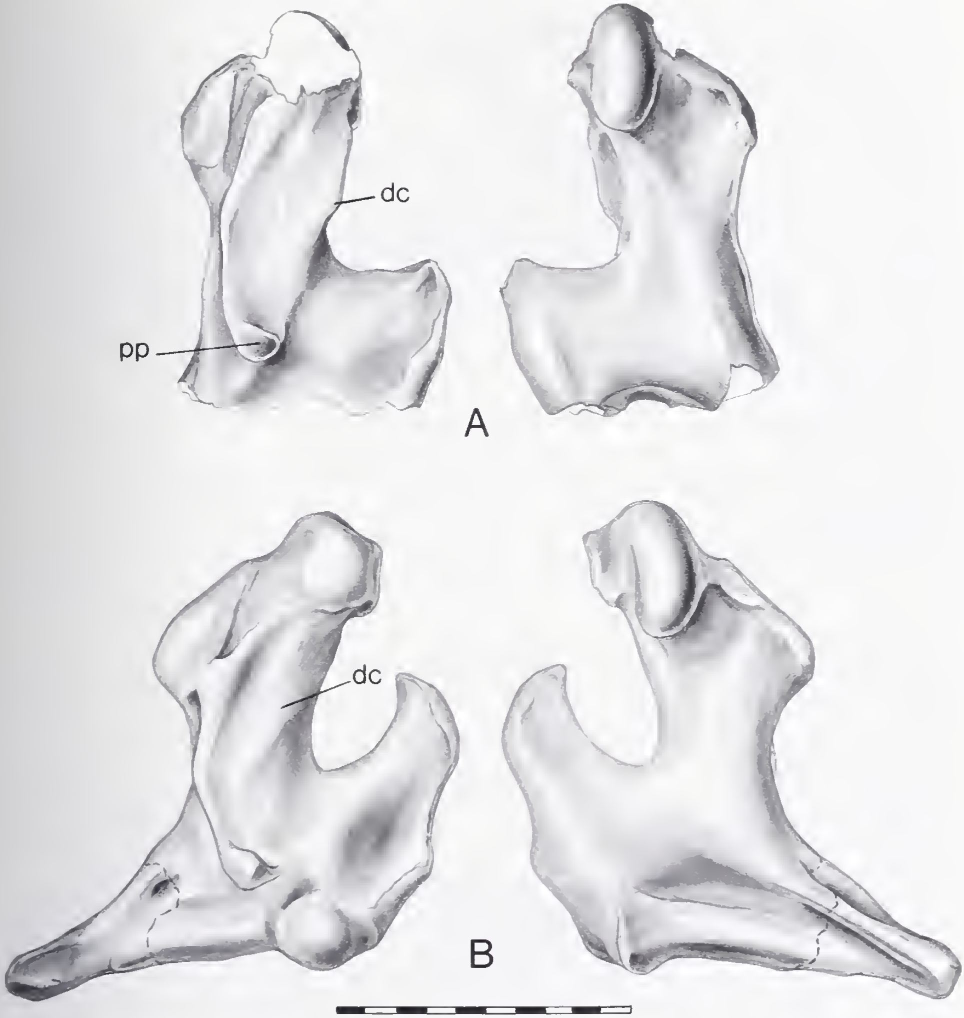


Fig. 6.—Left humeri of epoicotheriids. (A) ?*Tetrapassalus* sp., CM 62653, from Powder Wash, Utah (Bridgerian), in anterior and posterior views (distal end incomplete); (B) *Epoicotherium unicum,* USNM 299906; medial epicondyle restored from USNM 299907. Abbreviations: dc—deltoid crest; pp—pectoral process. Scale is 10 mm.

Bony Pelvis: A fragment of the pelvis includes the acetabulum and the body of the ischium to the ischial tuberosity. It does not appear to differ significantly from that of *Metacheiromys* as figured by Simpson (1931), but detailed study must await further preparation.

Femur: The holotype includes a nearly complete left femur (missing only part of the medial condyle) and a well-preserved distal right femur (Fig. 8A, D). Except for their smaller size, they generally resemble the femora of metacheiromyids and *Pentapassalus*: the head is hemispherical but the articular surface extends laterally on the proximal and posterior surface of the neck, the neck is broad and oriented almost horizontally and perpendicular to the shaft, the greater trochanter is prominent and projects proximal to the head, the lesser trochanter projects posteromedially, and a large third trochanter is situated slightly proximal to midshaft. In *Xenocranium,* by contrast, the greater trochanter is smaller (below the head) and the third trochanter relatively more proximal than in *Dipassalus* and other palaeanodonts. The trochanteric fossa, which is deep in metacheiromyids and *Pentapassalus,* is

Table 2.—*Measurements (mm) of selected humeral characters in some palaeanodonts. Abbreviations: DPC L, length of deltopectoral crest measured from greater tuberosity; Head B, mediolateral breadth of humeral head; Head L, proximodistal length of humeral head; Hum L, length of humerus from most proximal point to capitulum; Sup L, proximodistal length of supinator crest; e, estimated; lt, left; rt, right.*

Taxon, specimen no.	Hum L	DPC L	DPC L/Hum L	Head L	Head B	Head L/B	Sup L/Hum L
Propalaeanodon schaffi, PU 13928	38.8	26.4	0.68	9.6	7.1	1.35	0.48
Palaeanodon ignavus, USGS 4726	61.6	41.5	0.67	14.0	10.2	1.37	—
Metacheiromys marshi, USNM 26132, rt	42.4	32.4	0.76	9.6	7.7	1.25	0.46
Metacheiromys marshi, USNM 26132, lt	41.1	32.5	0.81	10.1	7.8	1.29	0.49
Metacheiromys dasypus, AMNH 11718 (holotype)	74.2	55.6	0.75	18.5	14.9	1.24	0.48
Alocodontulum atopum, UM 93740, rt	42.2	33e	0.78	11.5	7.8	1.47	—
Alocodontulum atopum, UM 93740, lt	40.9	31.5	0.77	11.8	8.0	1.48	—
Pentapassalus woodi, AC 2766 (holotype)	45.4	36.1	0.80	12.0	8.4	1.43	—
Pentapassalus pearcei, USNM 20028, rt (holotype)	36.7	28.3	0.77	9.5	7.0	1.36	0.55
Pentapassalus pearcei, USNM 20028, lt	37.0	28.0	0.76	9.5	7.1	1.34	—
Dipassalus oryctes, CM 43286	16.7	13.5e	0.81	5.0	2.8	1.79	0.50
Dipassalus oryctes, CM 43747, rt	—	—	—	4.8	2.4	2.00	—
Dipassalus oryctes, CM 43747, lt	—	—	—	4.9	2.5	1.96	—
?*Tetrapassalus* sp., CM 62653	—	10.4e	—	4.1e	2.2	1.86	—
Epoicotherium unicum, USNM 299906	15.5	13.1	0.85	5.6	2.5	2.24	0.61
Epoicotherium unicum, USNM 299907	15.1	13.0	0.86	5.4	2.2	2.45	0.60

very shallow in *Dipassalus,* as it is in *Xenocranium* (Rose and Emry, 1983: fig. 15A), *Manis,* and recent edentates, perhaps indicating de-emphasis on the obturator and gemelli muscles (lateral rotators of the femur).

The distal femur is relatively broad and anteroposteriorly flat. The patellar groove is broad and shallow, but less so than in *Xenocranium* (Rose and Emry, 1983: fig. 15B, C). The medial condyle of the distal femur does not project much farther distad than the lateral condyle, consequently *Dipassalus* lacks the valgus at the knee (knock-knee) that is characteristic of *Xenocranium,* but not reported in any other palaeanodonts. The femoral condyles are directed posteriorly, suggesting a habitually flexed knee.

Tibia and Fibula: The tibia and fibula are firmly synostosed both proximally and distally, much as in dasypodids, and the tibia is laterally compressed proximally but mediolaterally broad distally (Fig. 8B, C, E). The shafts are separate and, to judge from the short sections preserved, bowed apart from each other for most of their length. Among palaeanodonts, only *Xenocranium* is known to have the tibia and fibula co-ossified at both ends (Rose and Emry, 1983). Distal fusion of these bones occurs variably in *Palaeanodon,* perhaps in old individuals (Matthew, 1918; Simpson, 1931), but such synostosis is otherwise unknown in palaeanodonts. It is, however, fairly widespread among fossorial mammals (Barnett and Napier, 1953) and is often associated with use of the hind limbs for digging or pushing sediment loosened by the forelimbs (as in the dasypodid *Chlamyphorus*; Rood, 1970).

An anterolateral tubercle is present on the proximal fibula just below the head; it may mark the origin of the peroneus longus muscle, which attaches in this region in dasypodids (Macalister, 1873).

The distal crural articular surface is broad and comparatively shallow, but synostosis of the prominent fibular malleolus to the distal tibia adds stability to the cruro-astragalar joint.

Astragalus: A right astragalus included with the holotype resembles that of other palaeanodonts in being relatively broad and flat (Fig. 9). The trochlea is shallow and broader than in *Palaeanodon* but not as broad as in *Pentapassalus,* in which the trochlea is also relatively shorter proximodistally (Table 1). On the ventral aspect, the calcaneal facets show less relief than in *Palaeanodon.* The posterior calcaneal (ectal) facet, especially, is less concave, and the astragalar sulcus shallower than in *Palaeanodon.*

Discussion.—Although incompletely known, the material described here unquestionably represents a type of palaeanodont not known before. Whereas taxa named up to now seem to belong clearly to either the Metacheiromyidae (characterized by greater tooth reduction including development of an edentulous

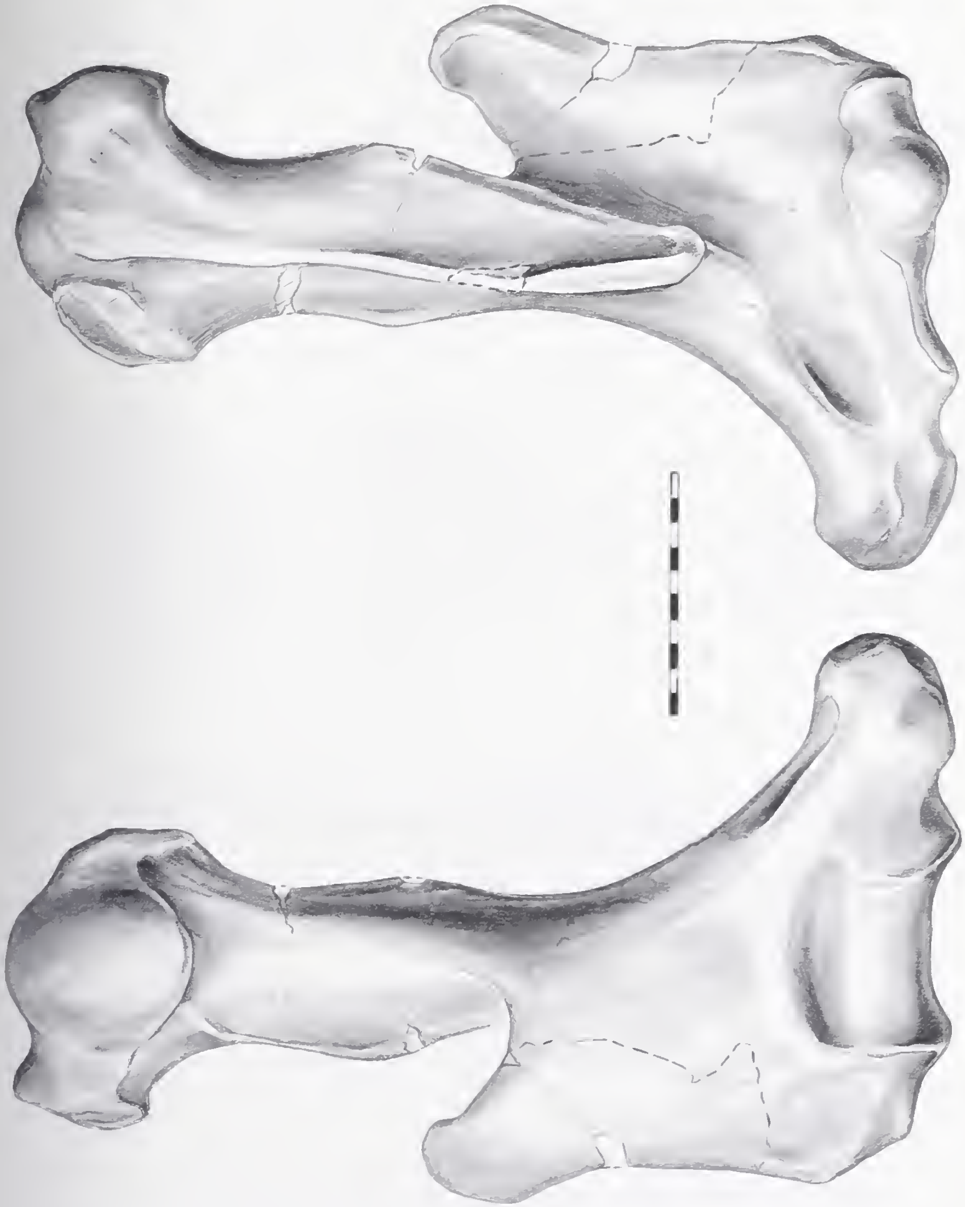


Fig. 7.—Left humerus of *Pentapassalus pearcei,* USNM 20028 (holotype; partly restored from right humerus), in posterior and anterior views. Scale is 10 mm.

posterior part of the dentary) or the Epoicotheriidae (typified by simple teeth that extend to the back of the dentary, coupled with a more specialized, fossorially adapted skeleton), the systematic position of *Dipassalus* is less obvious. Its extreme tooth reduction more closely approximates the condition in advanced metacheiromyids, while the postcranial skeleton is more like that of specialized epoicotheriids. Thus, whatever its relationships, *Dipassalus* must have evolved

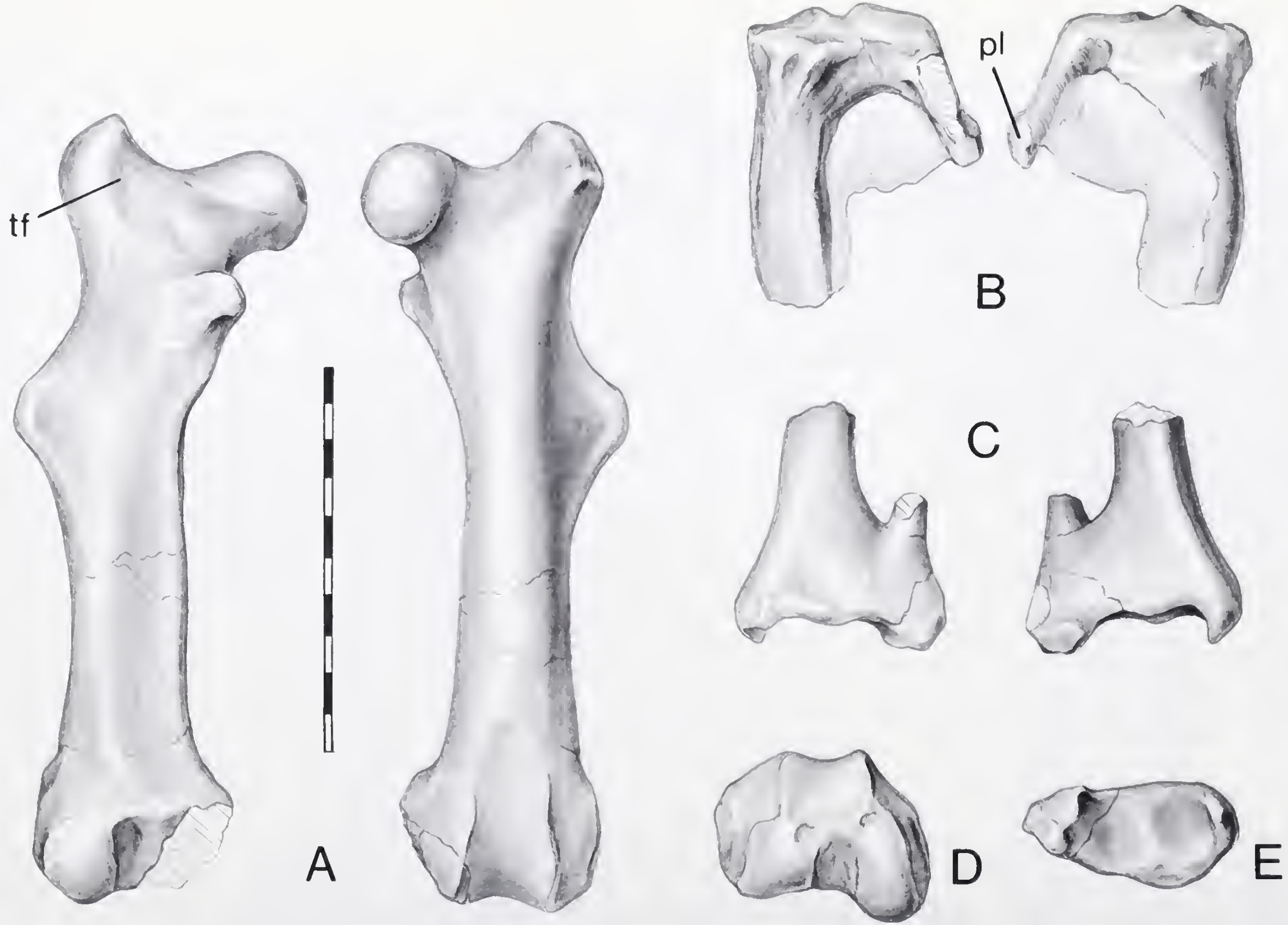


Fig. 8.—Hind limb elements of *Dipassalus oryctes*, new genus and species, CM 43286 (holotype). (A) Left femur in posterior and anterior views; (B) proximal right tibiofibula in posterior and anterior views; (C) distal right tibiofibula in posterior and anterior views; (D) distal right femur in distal view; (E) distal right tibiofibula in distal view. Abbreviations: pl—tubercle for ?peroneus longus origin; tf—trochanteric fossa. Scale is 10 mm.

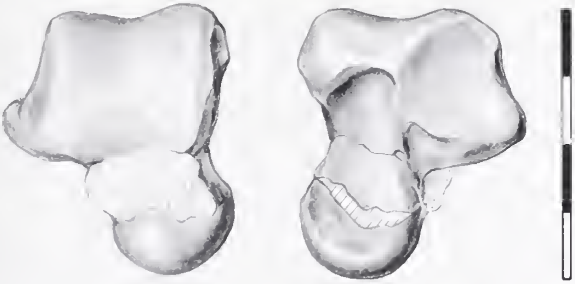


Fig. 9.—Right astragalus of *Dipassalus oryctes*, new genus and species, CM 43286 (holotype). Scale is 4 mm.

certain very derived aspects of its skeleton in parallel with one or the other family of palaeanodonts.

Dipassalus oryctes is here tentatively allocated to Epoicotheriidae on the basis of several derived characters of the dentition and skeleton it shares with members of that family (Fig. 10). In many postcranial characters, *D. oryctes* exhibits a structural stage intermediate between *Pentapassalus* and *Epoicotherium*; however, its greatly reduced dentition precludes such a phylogenetic position. Possession of a reduced number of vestigial peglike teeth was independently derived in each family (Simpson 1931, 1959; Rose and Emry, 1983) and would not prevent relationship with Metacheiromyidae; however, the degree of size reduction of the postcanines is greater in metacheiromyids (even those with more teeth), suggesting that *Dipassalus* belongs with the dentally more conservative group. Moreover, other characters—e.g., aspects of humeral morphology, reduction of femoral trochanteric fossa, synostosis of tibiofibula (Fig. 10, characters 10–14)—are derived within the Epoicotheriidae. Implicit in this tentative assignment is acceptance that the further loss of postcanines and concomitant development of an edentulous posterior dentary (characters 19, 20) evolved independently in *Dipassalus* and some metacheiromyids. A less likely alternative is that *Dipassalus* was a very derived metacheiromyid in which characters 10–14 evolved convergently in progressive members of both families.

Dipassalus was a small palaeanodont very close to the size of the fairy armadillo, *Chlamyphorus* (about 100 g). Among palaeanodonts only the epoicotheriids *Tetrapassalus* and *Epoicotherium* were as small. In known features, its skeleton is more fossorially specialized than metacheiromyids and *Pentapassalus*, but not as derived as *Xenocranium* and *Epoicotherium*. Like the latter two genera, *Dipassalus* may have been subterranean (as suggested by its diminutive size), but existing evidence is not definitive. What can be determined is that the forelimb modifications of *Dipassalus*, as seen in the humerus, are characteristic of specialized "terrier diggers" or "scratch diggers" (e.g., Reed, 1951; Hildebrand, 1985). The anatomy of the cervicothoracic spine provides further evidence that *Dipassalus*, like *Epoicotherium*, can be described as a "parasagittal head-and-forelimb digger," resembling the recent chrysochlorid *Eremitalpa* in digging behavior (Gasc *et al.*, 1986).

CONCLUSIONS

Paleomammalogists are accustomed to delineating and recognizing taxa by details of dental morphology; however, in forms such as palaeanodonts, where

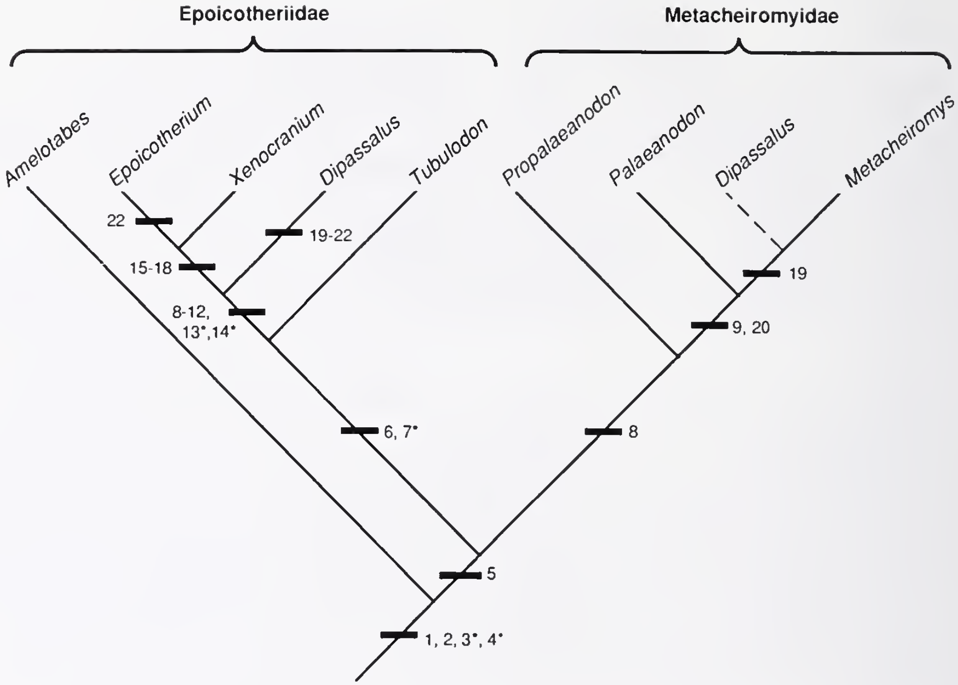


Fig. 10.—Hypothesis of relationships among Palaeanodonta showing proposed phylogenetic position of *Dipassalus* within Epoicotheriidae. A less probable alternative position among Metacheiromyidae is indicated by the dotted line. *Pentapassalus* and *Alocodontulum* are considered synonymous with *Tubulodon* in this diagram. *Tetrapassalus* is also omitted but is surely closely related to the *Epoicotherium-Xenocranium* clade. Characters marked by an asterisk (*) are not available for all taxa but are assumed present as indicated. Derived characters, not necessarily independent, are as follows: 1, cheek teeth with degenerate crown morphology and thin enamel; 2, dentary moderately shallow with medial buttress posteriorly; 3, canines triangular in cross section, occluding so as to form smooth honed facets on front of upper, back of lower; 4, humerus with long, elevated deltopectoral shelf and greatly expanded supinator crest; 5, cheek teeth reduced in size, single rooted or with roots coalesced into bilobed root (except P_4); 6, six or fewer lower postcanines (one or more postcanines lost); 7, olecranon relatively longer and metacarpals relatively shorter and more robust than in metacheiromyids; 8, postcanines generally reduced to single-rooted pegs; 9, five or fewer postcanines; 10, lesser tuberosity more distal and medially projecting; 11, humeral head proximodistally elongate; 12, deltopectoral crest reduced in elevation; 13, trochanteric fossa reduced; 14, tibia and fibula synostosed at both ends; 15, supinator crest extremely hypertrophied and with hooklike proximal projection; 16, deltopectoral crest extending further distally, with distinct pectoral tubercle at distal end; 17, cervical vertebrae 2–5 synostosed; 18, greater tubercle lower than humeral head; 19, generally two postcanines; 20, back of dentary edentulous; 21, deltoid tubercle prominent and projecting laterad; 22, bicipital groove covered by bone (osseous tunnel).

the dentition has clearly undergone extensive reduction and simplification, this usually important character is of questionable utility. We know little about the intraspecific variability in number, size, and spacing of cheek teeth in palaeanodonts, but it seems likely that variation would be high in groups in which teeth are substantially reduced and occlusal relationships simplified. We also remain ignorant of the extent of individual variation (or sexual dimorphism) in canine size and jaw depth. This variation obviously merits further study.

The Eocene Wind River Formation yields fossils of at least three genera of palaeanodonts—cf. *Palaeanodon, Tubulodon* (probably including *Pentapassalus*), and the new genus *Dipassalus*. Perhaps more than one species of the first two were present, but an assessment of precise species numbers based on existing evidence would be premature. The new material reported here not only confirms the presence of metacheiromyids (for the first time) as well as epoicotheriids in the Wind River Basin, it also reveals the existence of a new and unexpected, highly specialized fossorial palaeanodont. Derived characters of *Dipassalus* include a curious combination of traits that were formerly believed to be restricted to either Metacheiromyidae or Epoicotheriidae but not both, thus indicating that evolution within the Palaeanodonta was more complex than previously envisioned.

ACKNOWLEDGMENTS

For access to comparative fossil specimens we thank T. M. Bown (USGS), M. C. Coombs (AC), R. J. Emry (USNM), P. D. Gingerich (UM), M. C. McKenna (AMNH), and J. H. Ostrom (Yale). We are particularly indebted to Elaine Kasmer for her painstaking execution of the figures. We also thank T. M. Bown, R. J. Emry, R. E. Heinrich, and L. M. Witmer for discussion and/or review of the manuscript. Research or field work that produced specimens described or mentioned here has been supported by the John J. Hopkins Fund and NSF grants BSR-8215099 and BSR-8500732 (to KDR), and BSR-8402051, BSR-8709242 and BSR-8709242 Supplement (to LK and RKS). Geological research for this project was supported through NASA grant NAGW-0949 to RKS and LK.

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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 1, Pp. 83–91 27 February 1991

VALIDATION OF THE GENUS *ROWLEYELLA* WELLER, 1911, AND DESCRIPTION OF A NEW GENUS (BRACHIOPODA: ATHYRIDIDA)

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Abstract

The small Lower Carboniferous camarophorellid genus *Rowleyella* Weller, 1911, was placed in subjective synonymy with the Middle Devonian genus *Camarospira* Hall and Clarke, 1893, by Boucot *et al.* (1965). Transverse serial sections of a silicified chert-filled specimen reveal that the genus is internally distinctive and more similar to *Camarophorella* than to *Camarospira*. In *Rowleyella* the dorsal adductor platform is abbreviated and modified to form two chambers just below the cardinal plate. Thus, *Rowleyella* is morphologically distinct from both *Camarospira* and *Camarophorella* and represents a valid genus.

A new genus is proposed for the athyridid species *Athyris crassicardinalis* White, 1860, from the late Kinderhookian (Lower Carboniferous) of Iowa and Missouri. This genus differs from another Kinderhookian athyridid with which it is sometimes associated, *Planalvus* Carter, 1971, mainly in having reversed valve inflation.

Introduction

When I studied the late Kinderhookian and early Osagean brachiopod faunas of Iowa and Missouri (Carter, 1968, 1971, 1972), I accumulated specimens of poorly known genera and species, but did not deem it useful to redescribe them at that time. However, the prospect of a revised edition of the *Treatise on Invertebrate Paleontology* makes it prudent to present new generic information that is pertinent to the revised *Treatise*. Therefore, description of these specimens now assumes greater urgency. The present paper consists of two disparate parts. The first part comprises a redescription, reillustration and validation of the genus *Rowleyella*, which was misdiagnosed in the original *Treatise*. The second part consists of the description of a new athyridid genus.

The Genus *Rowleyella* Weller, 1911

This genus was described by Weller (1911:447) as follows: "Shell terebratuliform, with the valves subequally convex. The beak of the pedicle valve perforated by a subcircular foramen which encroaches wholly upon the umbonal region, the delthyrium broadly triangular and wholly closed. Internally each valve is supplied with a strong median septum which, in the pedicle valve, reaches nearly to the center of the valve, that of the brachial valve being somewhat shorter." This brief description was not accompanied by illustrations or genus comparisons *per se*, although Weller took care to discuss possible relationships of his new genus with the terebratulids, pentamerids, and camarophorellins. He concluded that it was most similar to the genus *Camarophorella* Hall and Clarke, 1893, noting that it differed in showing no evidence of a "brachial platform" (dorsal adductor platform or dorsal shoe-lifter process).

Weller (1914) essentially repeated this description but added that he had detected laterally directed spiralia, consisting of about four whorls each. He repeated his assertion that *Rowleyella* was closely related to *Camarophorella*, differing mainly in lacking the dorsal adductor platform on the floor of the valve. He suggested that "If a platform of this sort is present, its margins are entirely free."

This monotypic genus is known only from silicified specimens from the Burlington Limestone (lower white chert beds) in and near Louisiana, Pike County, Missouri. Rowley's two syntypes are illustrated herein (Fig. 1A–D). These specimens have not been photographically illustrated before. Rowley (1900: pl. 5, fig. 51–53) provided crude drawings of one of them and Weller (1914: pl. 82, fig. 64–69) used non-type specimens for his photographs.

Although all of these specimens are silicified and usually filled with coarse quartz crystals, some specimens retain the internal structures as soft white chert that contrasts well with the nearly clear quartz matrix. A medium-sized specimen was successfully sectioned, providing additional details of the internal morphology. A jugum has still never been observed but enough new information was obtained by sectioning to allow a more complete diagnosis, and to confirm its close relationship with the genus *Camarophorella,* not *Camarospira.*

Family Meristellidae Waagen, 1883
Subfamily Camarophorellinae Schuchert, 1929
Genus *Rowleyella* Weller, 1911
Fig. 1A–Q, 2

Rowleyella Weller, 1911:447.
Rowleyella: Weller, 1914:462.
Rowleyella: Schuchert, 1929:109.
Rowleyella: Likharev, 1960:284.
Camarospira Hall & Clarke, 1893 (part): Boucot, Johnson, and Staton, 1965:H658.
Camarospira Hall & Clarke, 1893 (part): Grunt, 1986:42.

Type species (by original designation).—Terebratula fabulites Rowley, 1900:265.

Diagnosis.—Small, elongate, subequally biconvex, with slightly flattened venter and weakly uniplicate anterior commissure but lacking fold and sulcus; foramen circular to ovate; delthyrium closed by dorsal umbo and narrow deltidial plates; ornament lacking except for very fine growth lines and coarser, irregularly spaced growth varices; interior of ventral valve with spondylium supported by strong high median septum and short mystrochial plates; dorsal interior with concave or shallow V-shaped cardinal plate supported by strong short median septum; dorsal adductor platform originates at dorsal beak; sides of dorsal adductor platform extending to floor of valve extremely short; ventral portions of adductor platform attached to dorsal surfaces of inner socket ridges, forming two short subtriangular chambers directly under cardinal plate; spiralia directed laterally, composed of four whorls each; jugum unknown; shell substance impunctate; inner shell surfaces of both valves finely and densely papillose as in *Camarophorella.*

Development of the dorsal muscle platform.—The Camarophorellinae is a small group of three genera of meristelloid athyridids endemic to North America. They are characterized by having a ventral spondylium, a dorsal median septum, and a complex jugal structure that includes a ventral process that splits ventrally, forming two posteriorly recurved loops, the distal ends of which fuse with the jugum dorsally. The earliest genus *Camarospira,* of Middle Devonian age, lacks a dorsal muscle platform and its jugum is unknown. Hence this genus is not included in the following discussion.

In the late Famennian the earliest species of *Camarophorella* appears, *Camarophorella buckleyi* (Rowley, 1908) from the Louisiana Limestone of Missouri. This

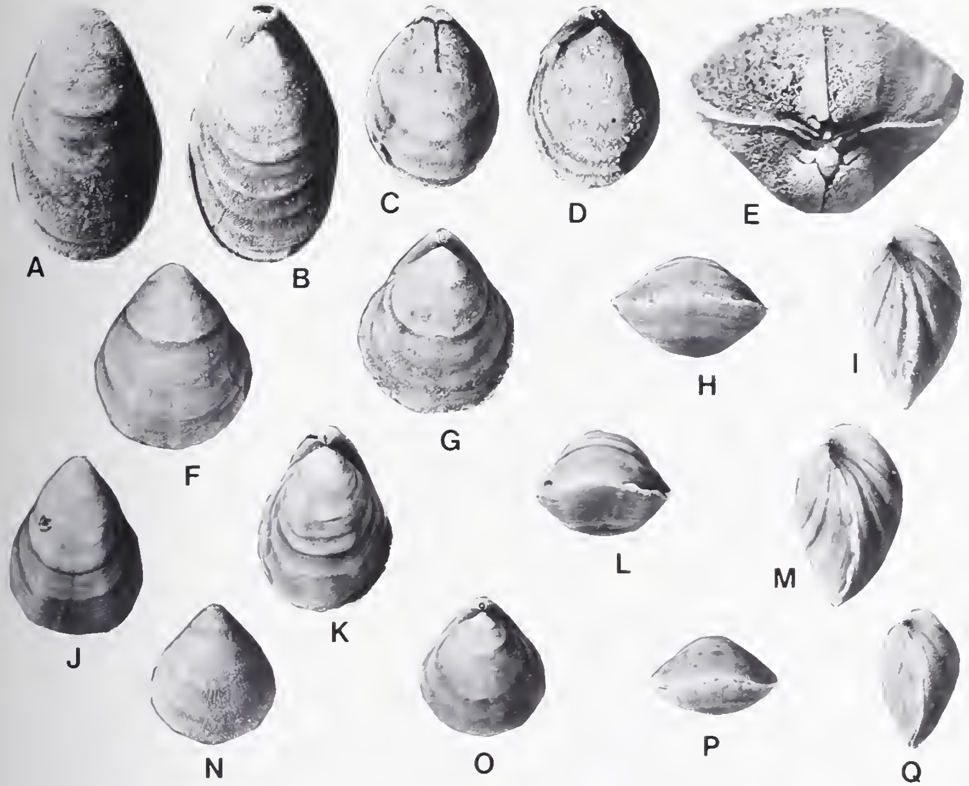

Fig. 1.—*Rowleyella fabulites* (Rowley). A–D, the two syntypes from the Burlington Limestone (lower white chert) at Louisiana, Pike County, Missouri. A, B, ventral and dorsal views of the largest syntype, University of Illinois RX-165B. This specimen is probably the one illustrated by Rowley (1900: pl. 5, fig. 51–53). It is a juvenile *Cranaena* sp., ×5. C, D, ventral and dorsal views of the lectoholotype, University of Illinois RX-165A, selected herein, a small, spalled silicified specimen (most of the shell of the ventral valve is removed clearly showing the ventral median septum), ×5. E–Q, four specimens from the Burlington Limestone (lower white chert) at the City Quarry, Louisiana, Pike County, Missouri. E, posterior view of a silicified natural internal mold showing the mystrochial plates and very short dorsal shoe-lifter process, CM 34945, ×8. F–Q, ventral, dorsal, anterior and lateral views of three well-preserved, complete specimens, CM 34946–34948, ×3.

species ranges into the earliest Carboniferous Glen Park Formation in Missouri and Illinois (Carter, 1988). Other early Carboniferous species are: *Camarophorella lenticularis* (White and Whitfield, 1862), the type species, from the Prospect Hill Sandstone of southeastern Iowa and possibly the Chouteau Limestone of Missouri; *C. dorsata* Carter, 1967, from the Chappel Limestone of central Texas; and *C. mutabilis* Hyde, 1908, from the Logan Formation of Ohio. *Camarophorella buckleyi* differs from the early Carboniferous species in one important respect, namely, the dorsal muscle platform originates well in front of the cardinal plate. Because the interior of this species has not been illustrated serial sections of it are shown in Fig. 3. Weller (1914: pl. 82, fig. 63) illustrated one of the syntypes of *C. lenticularis* which shows the dorsal adductor platform originating anteriorly, probably just in front of the cardinal plate, but not as far forward as in *C. buckleyi*. Carter's (1967: fig. 17) illustration of *C. dorsata* showed the dorsal adductor

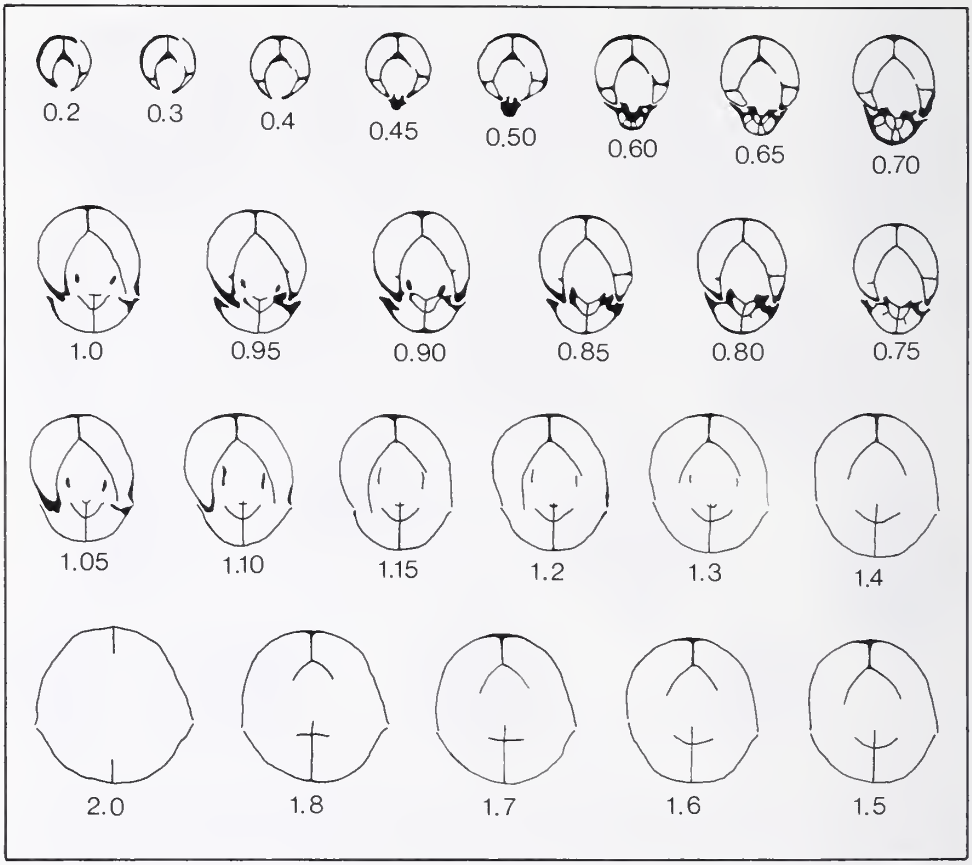

Fig. 2.—Transverse serial sections of a small silicified specimen of *Rowleyella fabulites* (Rowley), CM 34949, Burlington Limestone (lower white chert), from the City Quarry, Louisiana, Pike County, Missouri. Numbers refer to distance in mm from ventral beak. ×6.

platform placed posteriorly and dorsal to the cardinal plate, but not at the beak. Hyde (1908: pl. 6, 8, 9) showed specimens of *C. mutabilis* in which the dorsal adductor platform seemingly originates at or very near the dorsal beak.

Thus, the dorsal muscle platform in the genus *Camarophorella* migrates posteriorly through time, from well in front of the cardinalia, ultimately originating near the dorsal beak. In the genus *Rowleyella* this posterior migration is carried one step farther and culminates with the almost complete loss of the dorsal shoe-lifter process and development of a double chamber under the cardinal plate, fused to the dorsal surfaces of the inner socket ridges. The sides of the original shoe-lifter process are extremely short and are lost posteriorly, very near the dorsal beak. The large transverse plate seen in Fig. 2, sections 1.05–1.8, is homologous to the roof of the original shoe-lifter process and is analogous to the camarophorium in the stenoscismatoideans. In this manner the length of the adductors is greatly shortened.

Discussion.—Rowley (1900: pl. 5, fig. 51–53) illustrated only one of his two very small syntypes (University of Illinois, RX-165A, B) of *Terebratula fabulites,*

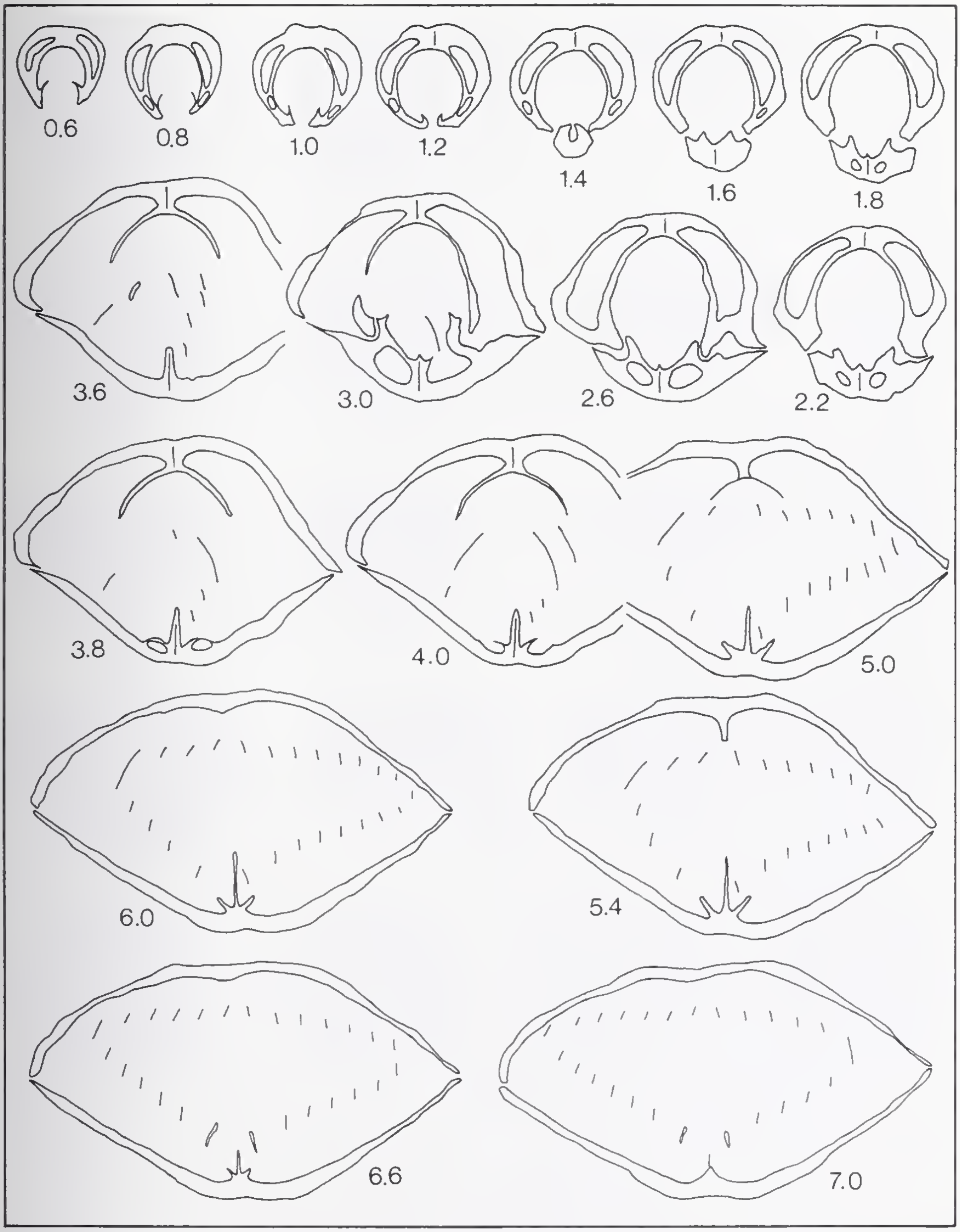

Fig. 3.—Transverse serial sections of *Camarophorella buckleyi* (Rowley), CM 34950, from the Louisiana Limestone, Louisiana, Pike County, Missouri. Note the anterior development of the dorsal shoe-lifter process, well in front of the cardinalia. Numbers refer to distance in mm from the ventral beak. ×4.

using three very small, crude line drawings at natural size. Weller (1914:464) studied Rowley's types and stated that the specimen illustrated by Rowley (University of Illinois, RX-165B) "has been carefully examined, and although the shell itself is intact, the presence of a median septum in each valve seems to be clearly indicated." I have also studied this specimen and conclude that the specimen Rowley illustrated appears to be a small specimen of *Cranaena,* a terebratulid. I find no evidence of the existence of a median septum in either valve, but the specimen has a labiate foramen and is obviously punctate (Fig. 1). However, the remaining syntype (University of Illinois RX-165A) is indeed a small, possibly juvenile, example of this small camarophorellid genus and is herein designated the lectoholotype. It is illustrated on Fig. 1C, D. Because Rowley's original name and description could apply equally well to either syntype, one could justifiably restrict the name *Terebratula fabulites* to the small terebratulid syntype. However, Weller's interpretation of this species is entrenched in the literature. Conservation of his concept of the species by designating the other syntype as lectotype is the most logical choice.

The number of known specimens of this genus is very small. At the time Rowley (1900) described this species he had only the two syntypes. He subsequently collected several more specimens which are now in the collections of the University of Illinois-Urbana. Weller (1914:464) described and illustrated two specimens which are now housed in the Field Museum of Natural History. Six specimens are in the collections of The Carnegie Museum of Natural History, four of which are illustrated here.

Neither Rowley (1900) nor Weller (1911, 1914) observed the presence of mystrochial plates in the pedicle valve of *Rowleyella fabulites.* These plates are easily seen in Fig. 1E and 2 (0.2–0.75). Their development and placement is comparable to that of the genus *Camarophorella.* These authors failed to observe the very short shoe-lifter process, or dorsal adductor platform, in the dorsal umbo. These plates are best observed in transverse sections (Fig. 2 [0.60–0.70]). The extremely short shoe-lifter process is fused with two nearly vertical plates attached to the dorsal surfaces of the inner socket ridges, forming a pair of subtrigonal chambers. The purpose of these chambers is not known but they probably functioned in much the same manner as the shoe-lifter process, that is, as a means of shortening the adductor muscles. Rudwick (1970:65) speculated that brachiopods with non-tendinous muscles might achieve greater muscular efficiency by means of shortening muscle length with various kinds of platforms. In this interpretation strongly biconvex brachiopods with non-tendinous muscles tend to develop muscle platforms. Once tendinous muscles appeared in a given stock, muscle platforms would tend to disappear.

Description of a New Genus

Family Athyrididae Davidson, 1881
Subfamily Athyridinae Davidson, 1881
Genus ***Densalvus,*** new genus
Fig. 4

Type species.—*Athyris crassicardinalis* White, 1860:229 (Lectoholotype designated herein, University of Michigan, Museum of Paleontology 66073).

Species assigned.—Monotypic.

Stratigraphic range.—Early Carboniferous (late Kinderhookian) of Iowa and Missouri.

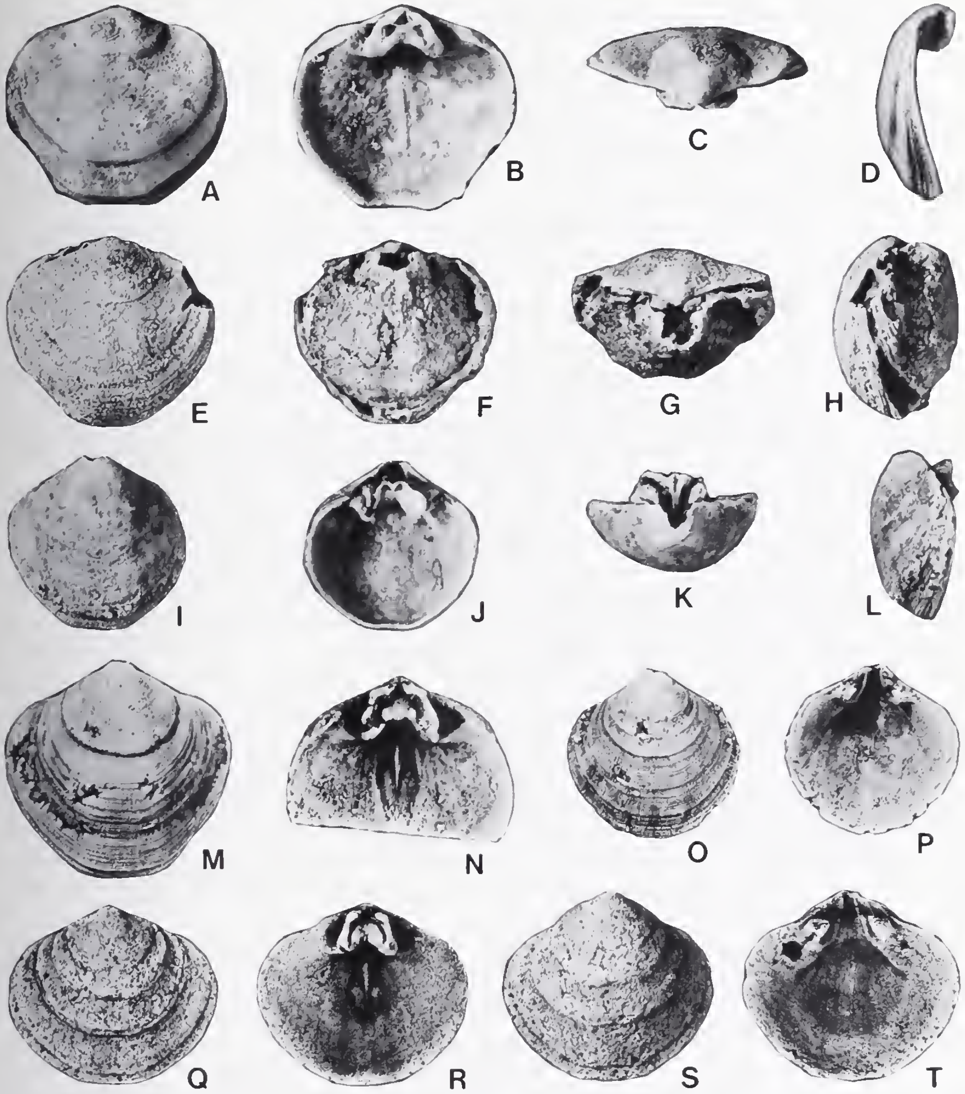

Fig. 4.—*Densalvus crassicardinalis* (White, 1860). A–L, three syntypes from the White Collection, University of Michigan, all from the Wassonville Dolomite at Burlington, Des Moines County, Iowa; A–D, dorsal, ventral, posterior and lateral views of a large dorsal valve, University of Michigan 66074; E–H, dorsal, ventral, posterior and lateral views of a silicified shell with a well-preserved dorsal valve but spalled ventral valve, University of Michigan 66075; I–L, ventral, dorsal, posterior and lateral views of the lectotype (selected herein, University of Michigan 66073), a small pedicle valve with dorsal cardinalia attached; M–P, three of Weller's illustrated specimens, including a large dorsal valve exterior, a large dorsal valve interior, and two views of a small ventral valve, respectively, from the Chouteau Limestone at Sedalia, Pettis County, Missouri, Field Museum of Natural History, Weller Collection UC 9817; Q–T, two views each of silicified dorsal and ventral valves, CM 34951 and CM 34952, from the Hampton Formation (Eagle City Limestone Member), near Legrand, Marshall County, Iowa; all ×3.

Etymology.—From the Latin *densus*—thick, and *alvus*—belly (feminine); referring to the thick ventral valve.

Diagnosis.—Small, unequally biconvex athyridids with strongly inflated ventral valve and weakly convex dorsal valve; dorsum flattened and venter well rounded; dental plates lacking; cardinal plate large, athyridid, not perforate; macro-ornament apparently simple but possibly weakly lamellose anteriorly; micro-ornament very finely and weakly capillate.

Description.—Small for the subfamily; outline variable, usually transversely subovate to subpentagonal; ventral valve much more inflated than dorsal valve; greatest width attained slightly posterior to midlength; lateral profile lenticular to guttate; hingeline short, curved; lateral extremities well rounded; dorsal fold and ventral sulcus lacking, dorsum flattened and venter well rounded instead; growth varices irregularly spaced; surface very weakly and finely capillate; growth lines very fine and almost evenly spaced, tending to be slightly lamellose anteriorly; other ornamentation not observed.

Ventral valve well inflated, thicker than opposite valve, with greatest convexity on venter in anterior view or anteriorly in lateral view; flanks weakly convex, sloping steeply to lateral margins; beak inconspicuous, not differentiated from umbo; foramen small, subcircular, mesothyridid; delthyrium filled by dorsal umbo and cardinal plate; beak ridges not present; interior with stout blunt teeth; dental plates lacking; muscle field large, moderately impressed, with low myophragm.

Dorsal valve weakly convex in both anterior and lateral views of most specimens, becoming thicker anteriorly in some gerontic shells, but usually much thinner than ventral valve; dorsum usually markedly flattened; dorsal umbonal region slightly inflated; beak sharply triangular, projecting into delthyrium, fused with cardinal plate; interior with flattened, subquadrate, imperforate cardinal plate fused to high stout socket ridges; brachidium unknown; dorsal adductor scars narrow, laterally depressed, medially raised, separated by low myophragm that extends from cardinal plate past midlength; ovarian pits present posterolaterally; shell substance impunctate.

Comparisons.—This new genus commonly occurs with another athyridid genus that is similar in size and general appearance, the genus *Planalvus* Carter, 1971. It differs from *Planalvus* mainly in having reversed valve convexity. In *Densalvus* the dorsal valve is thin and the ventral valve is thick; whereas in *Planalvus* the opposite is true, the dorsal valve is thick and ventral valve is thin. *Densalvus* seems to lack the spiny lamellae that occur in *Planalvus,* but I have not observed any well-preserved exteriors in *Densalvus crassicardinalis.* The unusual reversed valve inflation and lack of dental plates internally serve to distinguish this new genus from other members of the order.

Remarks.—Weller (1914:472) noted that *Athyris crassicardinalis* "is not a true member of the genus *Athyris,* neither can it be placed in another genus with any more certainty. It is not unlikely a representative of an undescribed genus. . . ." He hesitated to propose a new genus without definitive knowledge of its brachidium. I agree that the nature of the brachidium is important for systematic placement of this genus within a family. However, the unusual external and internal morphology of these shells is ample justification for proposing a new genus. Determination of its precise relationships to other genera in this group awaits discovery and description of the brachidium.

ACKNOWLEDGMENTS

I thank professors D. B. Blake of the University of Illinois-Urbana and D. B. Fisher of the University of Michigan for the loan of type specimens. F. D. Holland, Jr., and Peter Isaacson made useful suggestions for the improvement of this paper for which I am most grateful.

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REVIEWS

CENOZOIC MAMMALS OF NORTH AMERICA: GEOCHRONOLOGY AND BIOSTRATIGRAPHY. Michael O. Woodburne, ed. 1987. University of California Press, Berkeley. 336 p. $55.00.

THE PALEOGENE OF ASIA: MAMMALS AND STRATIGRAPHY. Donald E. Russell and Zhai Ren-jie. 1987. Volume 52 of Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre, Paris. 490 p. 300 FF.

In 1987 two landmark volumes were published which summarize the mammalian fossil record and the biostratigraphy derived from it for two continents. For North America, the entire Cenozoic mammalian biostratigraphic record was reviewed and related to established geochronology in *Cenozoic Mammals of North America: Geochronology and Biostratigraphy*. For Asia, the Paleogene mammalian biostratigraphic record was summarized and correlated, on both intercontinental and intracontinental scales, in *The Paleogene of Asia: Mammals and Stratigraphy*. Future historians of science and/or paleontologists inevitably will be tempted to compare and contrast these two volumes for the arbitrary reason that they happened to be published in the same year. In anticipation of the endeavors of these future generations of scholars, and to provide a sense of how the publication of these two volumes was received by a contemporary paleontologist, I record the following observations.

Cenozoic Mammals of North America: Geochronology and Biostratigraphy includes introductory and concluding chapters by the editor (Woodburne), a discussion of microtine rodent biostratigraphy by Repenning, and an essay outlining the usefulness of magnetic polarity stratigraphy by Lindsay et al. However, the "meat" of the volume is a group of chapters, each written by leading figures in the field, which together provide coverage of the entire Cenozoic mammalian biostratigraphy of North America. In general, these chapters are organized so that the North American provincial land mammal ages (NALMAs) that are covered correspond to traditionally recognized epochal boundaries, although the accuracy and precision of these correlations are, to variable degrees, unknown.

To a large extent, this uncertainty is due to the difficulty of correlating NALMAs with marine biochronologies, on which basis more precise intercontinental correlations might be established. Because the "classic" North American mammalian paleofaunas generally come from the continental interior, the difficulty of achieving correlations with the marine record can be readily appreciated. Fortunately, work currently in progress on newly discovered or less well-known mammalian faunas that can be correlated with the marine sequence (Westgate, 1988; Flynn et al., 1989) has already refined some of these correlations. It must be emphasized that these attempts to correlate NALMAs with epochal boundaries (via correlation with the marine record) are not merely academic exercises for those of us who would like to know, for example, whether we should refer to the Uintan NALMA as "middle" or "late" Eocene. Rather, these correlations are prerequisites for assessing very important paleobiological issues such as biogeographic hypotheses concerning centers of origin of higher taxa and direction of intercontinental dispersal of such taxa, and the relative ages of localities on different continents that contain taxonomically similar, but not identical, faunas.

An interesting and potentially useful convention is adopted by Archibald et al., who thoroughly review the first four Paleogene NALMAs (Puercan through Clarkforkian). They utilize an abbreviation of the NALMA in question combined with a number to indicate finer subdivisions within the NALMA. Thus, the Puercan NALMA is divided into zones Pu1–Pu3, the Torrejonian into zones To1–To3, the Tiffanian into zones Ti1–Ti6, and the Clarkforkian into zones Cf1–Cf3. These subdivisions are modified from the usage of Gingerich (1983), who also applied the convention to the succeeding Wasatchian NALMA. Gunnell (1989) has since extended its use to the Bridgerian and Uintan NALMAs. The brevity of this convention and the ease of communication it fosters suggest that it will become widely accepted. Despite these advantages, however, the ultimate utility of the subdivisions of the first four NALMAs used by Archibald et al. rests on the data on which they are based, and these are of variable quality (as the authors admit). In their probable order of decreasing utility, these data comprise interval-zones, lineage-zones, and acme-zones, respectively. In particular, the value of the lineage-zones, which are based on presumed lineages of plesiadapids, is contentious (R. C. Fox, personal communication).

The status of the later Cenozoic NALMAs forms the subject of most of the remainder of *Cenozoic Mammals of North America: Geochronology and Biostratigraphy.* These chapters summarize the biostratigraphy and geochronology of these NALMAs, and, perhaps more importantly, point to persistent lacunae in our understanding of them. From my reading of the book, it seems that much remains to be done, especially with respect to biostratigraphy of the middle Cenozoic NALMAs. Nevertheless, these chapters provide a handy reference, a quick point of entry to the primary literature, and the necessary springboard for future work on these problems. In accomplishing their stated goal of bringing the work of the Wood committee (Wood et al., 1941) up to date, Woodburne and the contributors to *Cenozoic Mammals of North America: Geochronology and Biostratigraphy* are generally successful.

The Paleogene of Asia: Mammals and Stratigraphy is, in one way, less ambitious than the volume just reviewed, in that the authors restricted themselves to only (!) the Paleogene part of the Cenozoic mammalian record. However, in other ways, this volume is actually more ambitious than the Woodburne volume: almost all of the local faunas discussed in *The Paleogene of Asia* are admirably placed in proper context by geographic and geologic maps, figures depicting stratigraphic sections, and thorough discussions of the geology of the rock units from which the faunas are derived. A comprehensive and up-to-date faunal list is provided for *each* assemblage, complete with synonymies and bibliographic references. Historical accounts of the discovery of the various mammalian faunas add further to the general interest of the volume. Because this book exhaustively reviews *all* of the Paleogene mammalian faunas known from the continent of Asia, from classic faunas like that from the middle Eocene of Irdin Manha to faunas that are currently represented by only a few isolated teeth, it is a contribution of monumental importance that is utterly without parallel. Some of the geological and historical accounts of the more poorly known faunas are the academic equivalent of a plea for help from a dying man; they will undoubtedly have the desired effect of stimulating renewed attention by the paleontological community at large.

To put the achievements of the authors of *The Paleogene of Asia* into adequate perspective, recall that the primary literature they review occurs in a significant fraction of the world's linguistic diversity (notably including Russian, Chinese, German, French, and English; I am sure I have missed additional languages that are represented in the bibliography). However, in many ways this volume is more than just a critical reference that summarizes knowledge of a subject in a concise and easily digestible way. Rather, it straddles the fence between being a reference work and a *bona fide* contribution to the primary literature. Many of the individual faunas reviewed here have never been treated in a holistic fashion, and much previously unpublished data collected by the authors and their colleagues appears for the first time. That *The Paleogene of Asia* ends by proposing the first coherent sequence of land mammal ages for the early Cenozoic of Asia amply testifies to the pioneering contribution the authors have made.

In summary, to paraphrase the words of Sir Isaac Newton, the accomplishments that are reviewed in *Cenozoic Mammals of North America: Geochronology and Biostratigraphy* are the result of the work of competent, dedicated scientists who had the benefit of standing on the shoulders of giants. In contrast, the accomplishments that are summarized in *The Paleogene of Asia: Mammals and Stratigraphy* are the work of the giants themselves.

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THE CARNEGIE
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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 2, Pp. 97–144 23 May 1991

CHELOMOPHRYNUS BAYI (AMPHIBIA, ANURA, RHINOPHRYNIDAE), A NEW GENUS AND SPECIES FROM THE MIDDLE EOCENE OF WYOMING: ONTOGENY AND RELATIONSHIPS

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Abstract

Chelomophrynus bayi, a new genus and species of rhinophrynid anuran, is based on a large sample from the middle Eocene (Bridgerian-Uintan) Wagon Bed Formation at Battle Mountain, in the Lysite Mountain Area, Hot Springs County, Wyoming. This rock unit is of lacustrine origin in this area. The specimens have been divided into six ontogenetic stages representing a developmental series ranging from tadpoles beginning metamorphosis to adults. These stages are defined by the appearance of processes, condyles, and elements, as well as the fusion of certain limb bones. An ontogenetic description is given for each element. The interrelationships of the rhinophrynids are discussed and the definition of this family is expanded. Revised diagnoses are given for *Rhinophrynus, R. dorsalis, R. canadensis,* and *Eorhinophrynus septentrionalis* and new material is referred to the latter. Character polarity for 15 characters is determined. Cladistic analysis of these characters suggests that *Chelomophrynus bayi* is more primitive than *Rhinophrynus* and that the precise relationship of the poorly known *Eorhinophrynus* cannot be determined at this time. The presence of two digging spades on each hind limb and a somewhat robust skeleton suggest that *Chelomophrynus bayi* is a burrowing anuran.

Introduction

A remarkable collection of a new genus and species of a middle Eocene rhinophrynid anuran was made in 1984 and 1986 by field parties from The Carnegie Museum of Natural History. The collecting site is a quarry located on Battle Mountain in the Lysite Mountain area, Hot Springs County, Wyoming, from which the fossil anurans were first reported by Bay (1969). The Carnegie Museum collection consists of several hundred partial to almost complete skeletons, isolated bones, and a mortality layer. A developmental series of tadpoles, subadults, and adults is present in this collection. Some complete and partial perciform fish also were collected from the frog quarry. This anuran collection is important because it is the largest for any known fossil rhinophrynid, contains the only complete fossil rhinophrynid, and is the largest sample of any fossil anuran species described from one locality in North America. It has provided a rare opportunity to study ontogeny and variation in this extinct anuran, thereby allowing a better understanding of evolutionary trends among the rhinophrynids.

Previously reported fossil and Recent rhinophrynids comprise three species in two genera, all from North and Central America. The extinct genus *Eorhinophrynus* ranges from late Paleocene to middle Eocene. *Eorhinophrynus septentrionalis,* the type specimen of which is an atlas (Hecht, 1959), is from the middle Eocene (Bridgerian) Bridger Formation at Tabernacle Butte, Sublette County, Wyoming. Estes (1975) figured a left fibulare (he mistakenly identified it as a tibiale) from the same locality which he referred to *E. septentrionalis.* He also described a humerus, sacrum, and tibiale (mistakenly identified as a fibulare) of *Eorhinophrynus* from the late Paleocene (Tiffanian) Fort Union Formation at the

Submitted 2 January 1990.

Fritz Quarry, Park County, Wyoming. Estes (1975) did not name this material as a new species or refer it to *E. septentrionalis*. *Rhinophrynus* has two species, one extinct and the other extant. *Rhinophrynus canadensis* (Holman, 1963, 1968, 1972) from the lower Oligocene Cypress Hills Formation, near Eastend, Saskatchewan, Canada, is represented by numerous isolated elements. The temporal range for the extant species *R. dorsalis* is from very late Pleistocene (Holman, 1969) to Recent. Its Pleistocene occurrence consists of isolated elements of one individual collected from Cueva de Abra, Tamaulipas, Mexico (Holman, 1969). Presently *R. dorsalis,* a highly adapted burrowing frog, inhabits dry tropical to subtropical forests along coastal lowlands in Central America, Mexico, and southern Texas (Fouquette, 1969; Foster and McDiarmid, 1983).

Institutional abbreviations are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; KU, The University of Kansas; MNHNP, Muséum National d'Histoire naturelle, Paris; MSU, Michigan State University; SMNH, Saskatchewan Museum of Natural History; UCMP, University of California Museum of Paleontology, Berkeley; UMMZ, University of Michigan Museum of Zoology; YPM-PU, Yale Peabody Museum.

GEOLOGY

The Lysite Mountain area is a large, dissected plateau composed of middle Eocene lacustrine strata which forms a divide between the Bighorn and Wind River basins (Bay, 1969; Krishtalka et al., 1987). These sediments, which lie unconformably on Pennsylvanian and Cretaceous beds, are currently mapped as part of the Wagon Bed Formation (Love et al., 1978; Thaden, 1979, 1980*a,* 1980*b,* 1980*c,* 1980*d,* 1980*e,* 1981; and Love and Christiansen, 1985), the type section of which is at Wagon Bed Spring in the Beaver Rim area. The Wagon Bed Formation is also found in the Badwater area, south of the Lysite Mountain area (Fig. 1).

The frog quarry is located near the top of a high escarpment at the northern end of Battle Mountain in a 5.5 m unit (upper sequence, unit 63 of Bay, 1969) comprised of interbedded sandstones and mudstones. The sandstones generally are fine grained and thinly bedded to homogeneous, whereas the mudstones are laminated. The fossil anurans are in the mudstones, except for the frog mortality layer, which occurs in a single sandstone layer.

Geological investigations of the Lysite Mountain area were reviewed by Bay (1969) who conducted a detailed study of this region. Since his work, reference to this area is found in Rohrer and Smith (1969), Bown (1982), Stucky (1984*a,* 1984*b*), and Krishtalka et al. (1987).

Bay (1969) recognized two informal, unconformable units, the lower and upper sequences. The lower sequence as recognized by Bay (1969, p. 14) consists of "... (1) a ... basal conglomerate consisting mostly of Mesozoic, Paleozoic, and Precambrian detritus, (2) analcimolite, (3) puffy, 'popcorn weathering' tufaceous claystone, (4) carbonaceous sediments, (5) 'red beds', (6) a particular type of calcite concretion, and (7) local areas of sediment distortion". The upper sequence is recognized by (Bay, 1969, p. 24) "... (1) a basal sandstone and conglomerate; (2) limestone, dolomite, and agate beds which are associated with some calcareous rocks; (3) authigenic feldspar; (4) tuff; (5) calcareous sandstone and siltstone concretions". Hard volcanic pebbles comprise the majority of clasts found in the basal conglomerate of the upper sequence.

Three types of lacustrine depositional environments were recognized by Bay

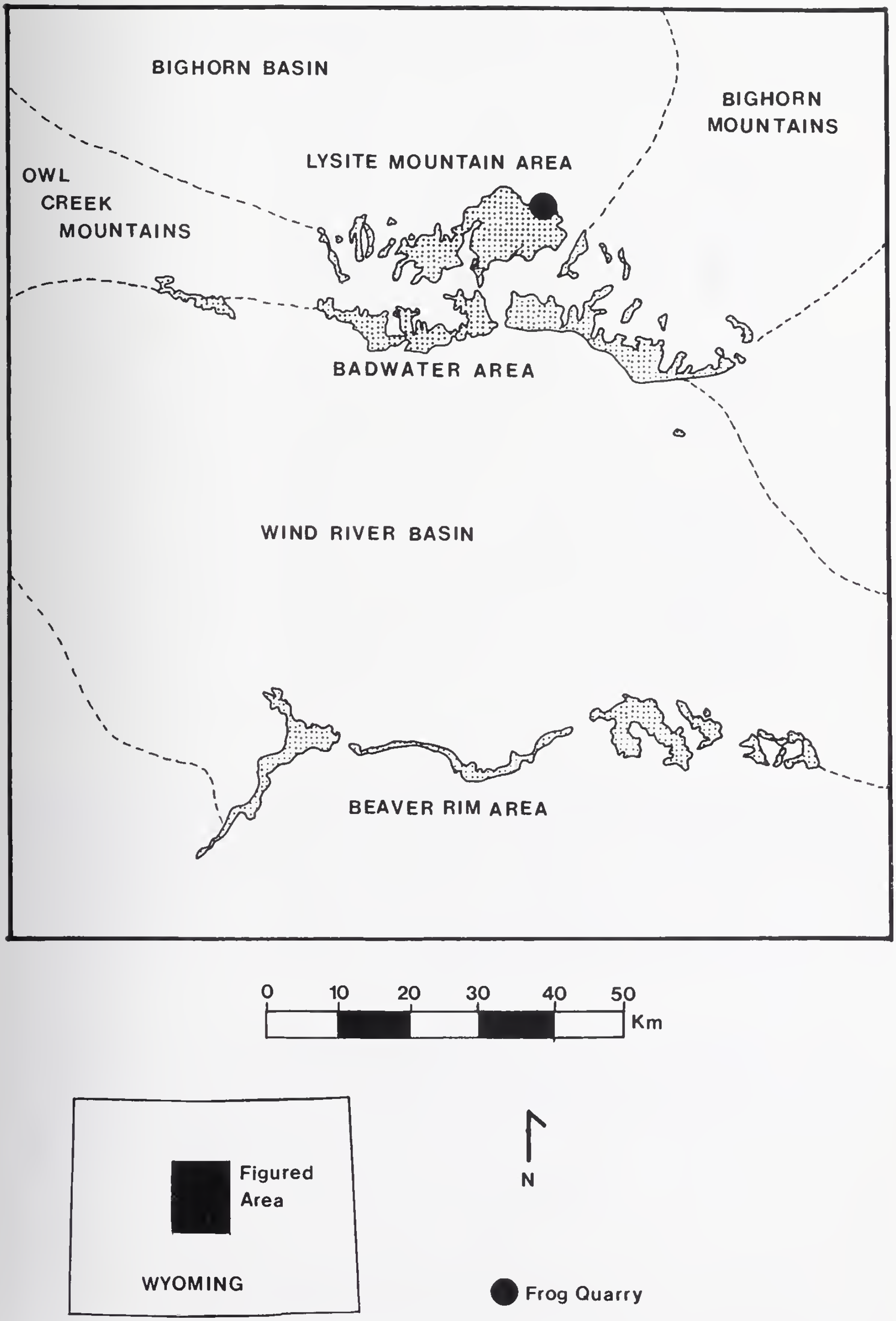


Fig. 1.—Map showing geographical extent of the Wagon Bed Formation (stipple) and location of frog quarry (circle).

Table 1.—*Vertebrate faunal list from the Lysite Mountain area (modified from Bay, 1969).*

Taxon	Lower sequence	Upper sequence
Osteichthyes		
Lepisosteidae	X	—
Amiidae	X	—
Ictaluridae	X	—
?*Mioplosus* sp.	X	—
Perciformes (new species)	—	X
Other Osteichthyes	X	X
Amphibia		
New genus and species	—	X
Reptilia		
Chelonia	X	X
Crocodilia	X	—
Squamata	X	—
Other Reptilia	X	X
Mammalia		
Carnivora	X	—
Hyopsodus sp.	X	—
Metarhinus sp.	—	X
Telmatherium cf. *T. cultridens*	X	—
?Brontotheriidae	X	—
Rhinocerotoidea	X	—
Dilophodon sp.	X	—
Forstercooperia grandis	—	X
Epihippus sp.	—	X
Equidae	X	—
Notharctus robustior	X	—

(1969) in the Lysite Mountain area. The first is a saline, alkaline lake environment in which authigenic silicate minerals formed from glass, zeolites, or volcanic material. The second is a Green River lake environment (following the depositional model proposed by Bradley, 1948), where carbonaceous sediments accumulated, forming oil shales. The third is a carbonate-rich lake in which limestones and some siltstone and tuff accumulated. The frog quarry lies in a sequence of rocks which most likely represents a shoreline facies of a carbonate-rich lake, the main body of which was located to the south (Bay, 1969).

AGE

At Battle Mountain a variety of fossils occur that are useful for determining the biostratigraphic age of sediments containing them (Table 1). Bay (1969) provided lists of invertebrates and plants referred to below. Gastropods were studied by Yen (1946), who concluded that the upper sequence could possibly be Bridgerian. Vertebrates have been studied by Gazin (1956) and listed by Love (1964) and Bay (1969). Based on the vertebrate fauna, Bay (1969) suggested that the upper part of the lower sequence through the upper sequence is late Eocene. An extensive fossil plant locality, the Rate Homestead flora, was discovered by Bay (1969). He included this locality in the lower sequence, but its relationship to other beds in the lower sequence could not be determined. MacGinitie (1969) concluded that this plant deposit is middle Eocene and comparable to the Green River flora.

The known mammalian fauna allows a more precise age determination for the sediments in the Lysite Mountain area. An incomplete jaw of the primate *Notharctus robustior,* as well as a tooth of a carnivore and a tooth of a rhinoceros, were collected by Carnegie Museum field parties approximately 137 m above the base of the lower sequence. The presence of *N. robustior* indicates a late Bridgerian (Twinbuttean; Robinson, 1957; Gazin, 1958; Krishtalka et al., 1987) to earliest Uintan (Shoshonian; Flynn, 1986) age for this locality. Near the top of the lower sequence, the remains of *Telmatherium* cf. *T. cultridens* and *Dilophodon* sp. were recovered (Tourtelot, 1948; Love, 1964; Bay, 1969). These taxa range in age from Bridgerian to Uintan (Krishtalka et al., 1987). Additional taxa are needed from the lower sequence to determine if the age is Bridgerian (Twinbuttean), Uintan (Shoshonian), or both.

The upper sequence mammalian fauna consists of teeth of *Metarhinus* sp., *Forstercooperia grandis,* and *Epihippus* sp. which were collected approximately 91 m above the base of the upper sequence. This fauna is not older than early Uintan, as indicated by the presence of *Metarhinus* sp. (Krishtalka et al., 1987), and is possibly earliest Uintan (Shoshonian; Flynn, 1986).

The beds containing the fossil rhinophrynid frogs described herein lie approximately 293 m above the base of the upper sequence and roughly 183 m above the *Metarhinus*-bearing unit. Thus the frog bed is no older than earliest Uintan, and it seems likely that it is younger than Duchesnean.

A radiometric age of 47.4 ± 1.5 my (recalibrated) was determined from a tuff lying approximately 46 m above the upper sequence mammal-bearing unit (Love, 1964). Bay (1969) noted that altered biotite in this tuff could cause the date to be anomalously old. However, if these beds are indeed earliest Uintan (Shoshonian), a date of 47.4 ± 1.5 my would be within reason.

MATERIALS AND METHODS

Over 300 specimens were recovered from the quarry. They consist of articulated, loosely articulated, and disarticulated skeletons (of which about 30 are nearly complete) as well as many isolated elements. A mortality layer was also recovered from a sandstone horizon in the quarry. Most of the bones are crushed; the ends of limb bones are more commonly crushed than the shafts. Specimens were collected by splitting mudstones along laminations, resulting in part and counterpart specimens that typically exhibit bone damage. Preparation, when necessary and feasible, was done using a dissecting microscope and a pin vise with beveled carbide or insect pins of varying thicknesses.

One hundred five of the best-preserved skeletons and isolated elements were measured and studied in detail. Several limb elements were removed from matrix to reveal otherwise obscured features. Illustrations were drafted with the use of the camera lucida. Measurements were taken with calipers under a zoom dissecting scope. Robustness refers to the width-to-length ratio of the skeletal element being discussed. These values are summarized in Table 2.

Descriptions of individual elements are composite unless otherwise noted. In the Description and Ontogeny sections, catalogue numbers in parentheses refer to specimens that best exhibit the features being discussed. The fossils were compared with Recent dry skeletons, cleared and stained specimens, and fossil specimens. In addition, the fossil tadpoles were compared with cleared and stained *Rhinophrynus dorsalis* tadpoles at Gosner (1960) stages 31, 34, 35, 36, 37, 42, 44, and 46. Phylogenetic analysis was done using PAUP 2.4 by David Swofford.

SYSTEMATIC PALEONTOLOGY

Class Amphibia
Order Anura
Family Rhinophrynidae

Revised diagnosis.—Can be distinguished from all other anuran families by the following combination of characters: supraorbital flange present; maxilla and pre-

Table 2.—*Statistics. All measurements in millimeters. n = sample number, x̄ = mean, SD = standard deviation.*

Element		*E.* sp.	*E. septentrionalis*	*C. bayi*	*R. canadensis*	*R. dorsalis*
Frontoparietal						
Length	n			21.0		15.0
	range			6.4–9.3		6.7–10.7
	$\bar{x}$			7.5		8.6
	SD			0.86		1.1
Width	n			21.0		15.0
	range			4.5–7.8		5.1–8.1
	$\bar{x}$			6.1		6.6
	SD			0.81		0.96
Robustness	n			15.0		15.0
	range			68.2–90.6		69.0–82.8
	$\bar{x}$			79.3		76.8
	SD			5.5		4.1
Nasal						
Length	n			8.0		9.0
	range			2.5–4.7		5.3–9.2
	$\bar{x}$			3.6		7.2
	SD			0.96		1.1
Premaxilla						
Length	n			6.0		10.0
	range			2.0–2.8		2.4–3.4
	$\bar{x}$			2.3		2.8
	SD			0.27		0.31
Height	n			6.0		10.0
	range			1.7–2.2		2.1–3.6
	$\bar{x}$			1.9		3.0
	SD			0.20		0.51
Maxilla						
Length	n			7.0		13.0
	range			6.0–8.4		5.2–7.9
	$\bar{x}$			7.1		6.3
	SD			0.86		1.4
Height	n			5.0		13.0
	range			1.9		1.7–2.9
	$\bar{x}$			1.9		2.3
	SD			0.0		0.33
Dentary						
Length	n			1.0		5.0
	range			5.6		4.7–8.2
	$\bar{x}$			5.6		6.2
	SD			0.0		1.3
Angulosplenial						
Length	n			4.0		7.0
	range			4.6–9.1		8.3–12.4
	$\bar{x}$			7.2		10.4
	SD			1.9		1.6
Parasphenoid						
Length	n			8.0		17.0
	range			7.8–10.5		8.3–11.8
	$\bar{x}$			9.1		9.7
	SD			0.90		0.96

Table 2.—*Continued.*

Element		*E.* sp.	*E. septentrionalis*	*C. bayi*	*R. canadensis*	*R. dorsalis*
Squamosal						
Length	n			1.0		4.0
	range			2.0		2.0–2.7
	$\bar{x}$			2.0		2.5
	SD			0.0		0.33
Height	n			1.0		11.0
	range			3.2		2.9–5.3
	$\bar{x}$			3.2		4.1
	SD			0.0		0.71
Sphenethmoid						
Length	n			4.0		18.0
	range			6.2–7.4		5.2–8.5
	$\bar{x}$			5.7		7.1
	SD			1.1		0.80
Width	n			5.0		12.0
	range			5.3–7.8		5.3–9.0
	$\bar{x}$			6.1		6.8
	SD			1.0		1.0
Robustness	n			4.0		11.0
	range			84.1–105.4		80.8–106.5
	$\bar{x}$			93.7		99.1
	SD			9.4		7.2
Parahyoid bone						
Width	n			1.0		9.0
	range			5.3		5.6–7.2
	$\bar{x}$			5.3		6.5
	SD			0.0		0.52
Posteromedial process						
Length	n			1.0		10.0
	range			4.9		4.2–8.3
	$\bar{x}$			4.9		6.4
	SD			0.0		1.1
Clavicle						
Length	n			7.0		17.0
	range			2.3–6.5		6.2–9.4
	$\bar{x}$			4.6		7.7
	SD			1.7		0.85
Scapula						
Length	n		1.0	15.0		17.0
	range		6.9	1.7–6.8		5.6–9.8
	$\bar{x}$		6.9	4.2		7.9
	SD		0.0	1.8		1.3
Coracoid						
Length	n			3.0		16.0
	range			1.8–4.4		3.9–7.0
	$\bar{x}$			3.5		5.6
	SD			1.5		1.0
Cleithrum						
Width	n			6.0		17.0
	range			3.4–9.9		6.9–13.4
	$\bar{x}$			6.5		9.8
	SD			2.4		1.7

Table 2.—*Continued.*

Element		*E.* sp.	*E. septentrionalis*	*C. bayi*	*R. canadensis*	*R. dorsalis*
Length	n			8.0		16.0
	range			8.0–14.4		10.7–21.8
	$\bar{x}$			11.0		15.5
	SD			1.9		3.2
Ilium						
Length	n			26.0		16.0
	range			5.0–23.6		15.0–30.1
	$\bar{x}$			11.9		23.0
	SD			4.8		4.6
Height	n			19.0		16.0
	range			1.4–7.0		6.5–12.8
	$\bar{x}$			4.2		13.3
	SD			2.0		3.8
Ischium						
Length	n			7.0		13.0
	range			1.9–3.0		2.5–5.6
	$\bar{x}$			2.4		4.2
	SD			0.43		1.0
Height	n			8.0		13.0
	range			2.1–6.0		4.5–8.8
	$\bar{x}$			4.2		6.9
	SD			1.1		1.4
Humerus						
Length	n	1.0		21.0		17.0
	range	12.6		3.9–12.1		8.1–18.9
	$\bar{x}$	12.6		9.5		13.6
	SD	0.0		1.8		3.5
Radioulna						
Length	n			19.0	3.0	18.0
	range			2.5–8.3	3.6–5.2	5.3–13.4
	$\bar{x}$			6.1	4.6	9.3
	SD			1.3	0.87	2.4
Width	n			13.0	3.0	18.0
	range			1.0–1.5	1.0–1.4	1.4–3.2
	$\bar{x}$			1.3	1.2	2.2
	SD			0.19	0.21	0.54
Robustness	n			13.0	3.0	18.0
	range			17.6–24.2	26.0–27.7	20.3–37.9
	$\bar{x}$			20.7	26.9	24.5
	SD			1.9	0.85	4.1
Femur						
Length	n			43.0		17.0
	range			3.0–17.2		11.3–21.4
	$\bar{x}$			10.9		16.7
	SD			3.4		3.3
Width	n			18.0		17.0
	range			0.60–1.4		0.9–1.9
	$\bar{x}$			1.0		1.3
	SD			0.28		0.31
Robustness	n			18.0		17.0
	range			8.0–22.7		7.1–9.7
	$\bar{x}$			12.0		8.1
	SD			4.7		0.67

Table 2.—*Continued.*

Element		*E.* sp.	*E. septentrionalis*	*C. bayi*	*R. canadensis*	*R. dorsalis*
Tibiofibula						
Length	n			37.0		18.0
	range			2.9–14.5		9.8–18.4
	$\bar{x}$			10.5		14.1
	SD			2.5		2.9
Width	n			18.0		18.0
	range			1.0–1.7		1.6–3.2
	$\bar{x}$			1.3		2.4
	SD			0.21		0.51
Robustness	n			18.0		18.0
	range			11.0–34.4		15.7–19.4
	$\bar{x}$			14.0		17.2
	SD			5.4		1.2
Fibulare						
Length	n		1.0	31.0		17.0
	range		7.6	1.8–8.8		4.6–9.5
	$\bar{x}$		7.6	5.9		6.9
	SD		0.0	1.6		1.4
Width	n		1.0	18.0		17.0
	range		1.2	0.50–1.3		1.3–2.5
	$\bar{x}$		1.2	0.90		1.9
	SD		0.0	0.20		0.40
Robustness	n		1.0	18.0		17.0
	range		15.8	12.7–38.9		23.4–32.0
	$\bar{x}$		15.8	17.5		27.3
	SD		0.0	6.8		2.4
Tibiale						
Length	n	1.0		25.0	2.0	17.0
	range	6.8		1.3–7.4	4.6–5.1	3.7–7.8
	$\bar{x}$	6.8		4.9	4.8	5.7
	SD	0.0		1.5	0.35	0.96
Width	n	1.0		12.0	2.0	17.0
	range	1.1		0.50–1.0	1.0–51.0	1.2–2.2
	$\bar{x}$	1.1		0.70	1.0	1.7
	SD	0.0		0.18	0.0	0.35
Robustness	n	1.0		12.0	2.0	17.0
	range	16.2		10.8–30.8	19.6–21.7	23.0–35.1
	$\bar{x}$	16.2		16.7	20.6	29.8
	SD	0.0		7.5	1.5	4.1
Forelimb						
Length	n			9.0		22.0
	range			6.4–19.4		5.6–32.2
	$\bar{x}$			14.8		19.1
	SD			3.6		8.9
Hindlimb						
Length	n			17.0		21.0
	range			9.4–40.0		9.8–48.9
	$\bar{x}$			30.0		31.5
	SD			6.2		13.7
$\frac{\text{Forelimb length}}{\text{Hindlimb length}} \times 100$	n			4.0		15.0
	range			47.0–53.3		51.4–65.8
	$\bar{x}$			48.9		60.4
	SD			3.3		4.6

maxilla edentate; palatine process of premaxilla absent; palatines absent; parahyoid bone present; eight imbricate, ectochordal, modified opisthocoelous presacral vertebrae; atlantal cotyles closely juxtaposed; atlantal neural arch elongate; presacrals I and II unfused; transverse process of second presacral vertebra hook shaped; free ribs absent; expanded sacral diapophyses; urostyle with bicondylar articulation with sacrum; arciferal pectoral girdle; clavicle overlying anterior end of scapula; humeral shaft strongly angulated; femur bearing lateral and medial crests; tibiale and fibulare fused proximally and distally; and prehallux and distal phalanx of first digit modified as bony digging spades. The following features (Duellman and Trueb, 1986) apply to the only known Recent rhinophrynid; these characters cannot be determined in the known fossil forms: omosternum and sternum absent; cricoid ring incomplete dorsally; two tarsalia present; normal phalangeal formula except for loss of one phalanx on first toe; m. sartorius distinct from m. semitendinosus, tendon of latter penetrates m. gracilis; m. glutaeus magnus lacks accessory tendon; m. adductor magnus lacks accessory head; vertical pupil; inguinal amplexus; Type I larvae; diploid chromosome complement is 22.

Genus *Eorhinophrynus* Hecht, 1959

Type species.—*Eorhinophrynus septentrionalis* Hecht, 1959.

Holotype.—AMNH 3818.

Horizon and locality.—Bridger Formation, locality 5, Tabernacle Butte, Sublette County, Wyoming, middle Eocene, Bridgerian.

Referred material.—Holotype and UCMP 113252, left fibulare; CM 46783, right exoccipital-prootic complex; CM 46784, right scapula; CM 46782, distal half of left humerus; CM 46785, proximal end of right tibiofibula.

Revised diagnosis.—Differs from all rhinophrynids in having atlantal neural arch that is laterally broad with square posterior margin. Differs from *Eorhinophrynus* sp. (*sensu* Estes, 1975) in having round humeral ball. Differs from *Rhinophrynus* in having well-developed lateral crest on humerus.

Description and discussion.—Isolated topotypic elements in the Carnegie Museum, referred herein to *E. septentrionalis,* include a right exoccipital-prootic complex, a right scapula, the distal end of a left humerus, and the proximal end of a right tibiofibula.

The exoccipital-prootic complex (CM 46783) is well preserved, lacking only the occipital condyle. It resembles that of the new genus and species described below in every aspect except that it is less robust.

The scapula (CM 46784) is cleft and relatively long. It has an articulating surface for the clavicle on the ventral end of the anterior edge. This indicates that the scapula is overlain anteriorly by the clavicle, a feature found in the families Leiopelmatidae, Discoglossidae, Rhinophrynidae, Palaeobatrachidae, and in one genus of Pipidae (*Pipa,* Duellman and Trueb, 1986). The Tabernacle Butte scapula is not a leiopelmatid, discoglossid, or palaeobatrachid because these have short, uncleft scapulae (Špinar, 1972; Duellman and Trueb, 1986). Nor is it that of a pipid as the pipid scapula is short (Cannatella and Trueb, 1988). The Tabernacle Butte scapula is therefore referred to the Rhinophrynidae.

The humerus (CM 46782) is fairly well preserved, although the medial epicondyl and distal ball are somewhat eroded. The ball is round, the olecranon scar medially situated, and the lateral and medial crests are moderately developed, long, and of subequal length. Enough of the shaft is preserved to determine that it is strongly angulated. The distal portion of the crista ventralis is present, but the degree of development cannot be determined because the proximal end is missing. A ridge extends from the crista ventralis to the medial epicondyle. The strongly angulated shaft indicates assignment to the Rhinophrynidae, a conclusion supported by the medially-situated olecranon scar and ridge running from the crista ventralis to the medial epicondyle.

Only the proximal end of the tibiofibula (CM 46785) is preserved. It is somewhat robust, suggesting rhinophrynid affinities, but this assignment is tentative.

Chelomophrynus, new genus

Type species.—*Chelomophrynus bayi,* new species.

Diagnosis.—Differs from all rhinophrynids in unique characters of broad, triangular alary process of premaxilla, anterior notch of maxilla, elongate posterior process of vomer, elongate postchoanal ramus of vomer, and laterally-oriented transverse processes of last three presacral vertebrae. Differs from *Eorhinophrynus* sp. in having round humeral ball and from *E. septentrionalis* in having atlantal neural arch that tapers posteriorly. Differs from *Rhinophrynus* in having well-developed lateral crest of humerus, shaft of femur slightly bowed, shaft of femur expanded directly proximal to distal condyle, and distal condyle of femur of equal length and width.

Etymology.—From the Greek *cheloma,* notch, and *phryne,* toad, in reference to the anterior notch on the maxilla.

Chelomophrynus bayi, new species

Holotype.—CM 46712 (Fig. 2): partially complete, articulated to loosely articulated skeleton of an adult at Stage VI. The skull is broken so that the right exoccipital-prootic complex is in alignment with the vertebral column; the rest of the skull, consisting of a left exoccipital-prootic complex, ?sphenethmoid, and parasphenoid, all incomplete, is displaced to the left. The postcranial skeleton includes the left humerus, vertebral column, sacral vertebra, urostyle, ilia, and left hind limb.

Hypodigm.—Holotype and CM 44480–44499, 46700–46711, 46713–46781, 46786–46799, 40827–40853.

Horizon and locality.—Northern end of Battle Mountain, in the Lysite Mountain area, Hot Springs County, central Wyoming, in sediments mapped as Wagon Bed Formation and considered middle Eocene. The frog quarry is believed to be Uintan. Specific locality data is on file in the Section of Vertebrate Paleontology, Carnegie Museum of Natural History.

Diagnosis.—As for genus.

Etymology.—*bayi,* in honor of Kirby Bay who discovered the first frog from this locality.

Description

These fossil anurans are most commonly preserved as partially complete, loosely articulated skeletons. The postcranial skeleton is articulated in numerous specimens, but a completely articulated skull has not been found. The frontoparietal is the most commonly preserved element, occurring in nearly and partially complete specimens, as well as being the most numerous isolated element. Limb bones commonly occur in partial specimens and as isolated elements. Hind limbs are more numerous than forelimbs.

Skull

Frontoparietal.—The robust frontoparietal is azygous, lacking a medial suture, fenestra, and pineal foramen. The shape varies greatly (Fig. 3) from roughly pentagonal to octagonal; in some frontoparietal bones the sides and angles are apparent, whereas in others the angles are rounded, resulting in a more oval shape. Some specimens possess a more robust frontoparietal than others. The shape of the anterior rostrum also varies ranging from long and pointed, to long and blunt, to short and blunt. The supraorbital flange is present. An incrassatio frontoparietalis (Roček, 1981) is not preserved.

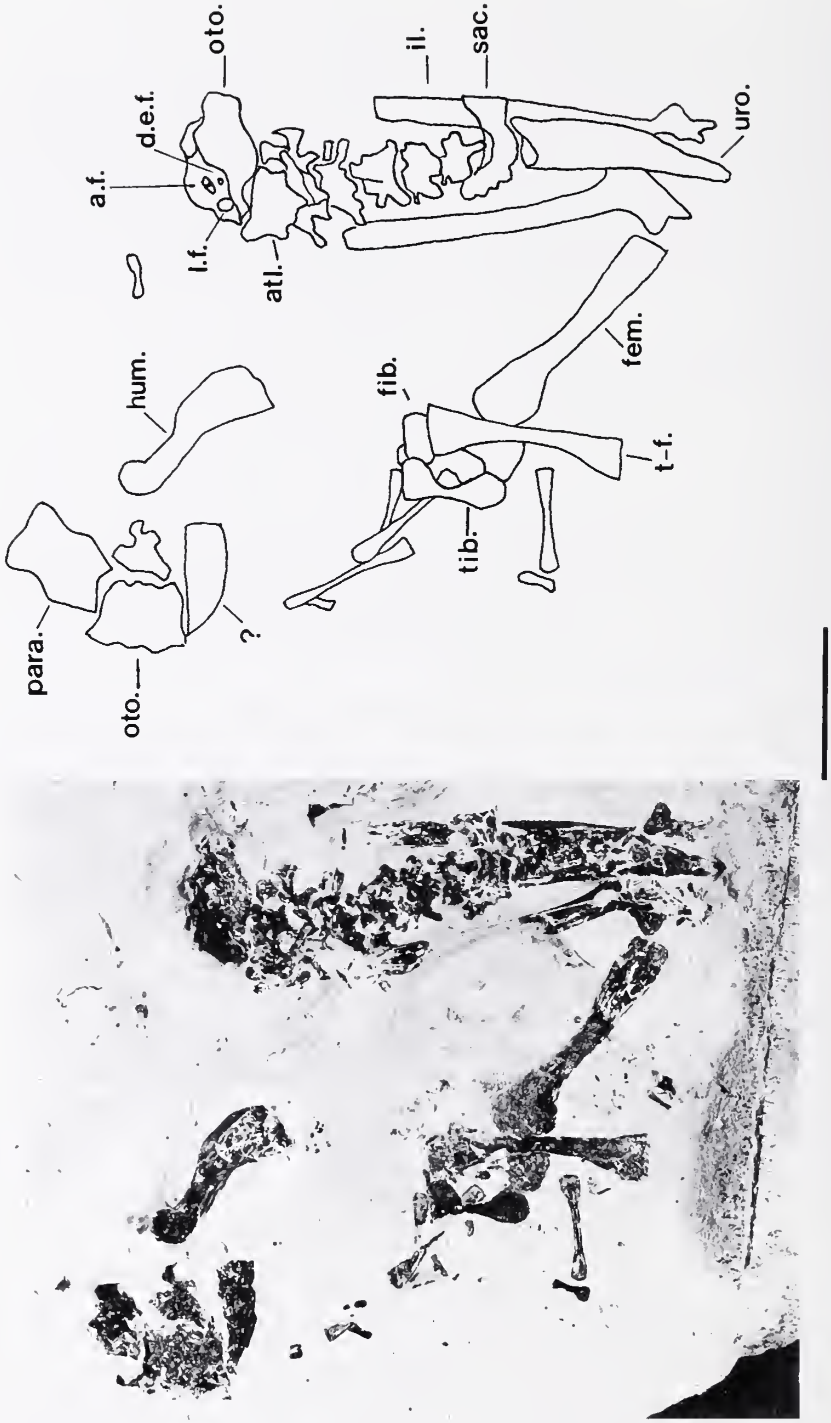


Fig. 2.—*Chelomophrynus bayi,* holotype, CM 46712, Stage VI. Abbreviations: a.f., acoustic foramina; atl., atlas; d.e.f., dorsal endolymphatic foramina; fem., femur; fib., fibulare; hum., humerus; il., ilium; l.f., lymphatic foramina; para., parasphenoid; oto., exoccipital-prootic complex; sac., sacral vertebra; t-f., tibiofibula; tib., tibiale; uro., urostyle. Scale bar = 10 mm.

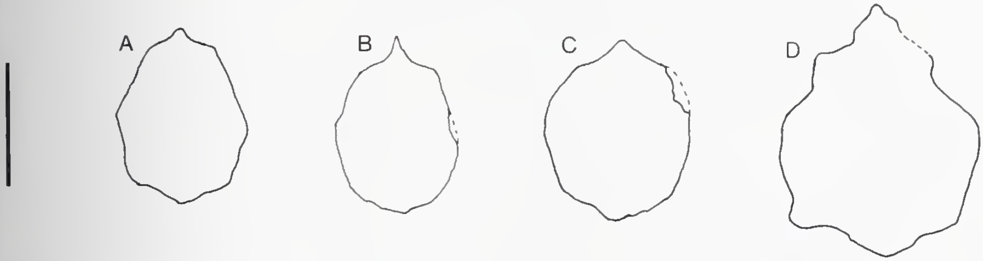


Fig. 3.—Variation in frontoparietal shape of *Chelomophrynus bayi.* (A) CM 46779; (B) CM 46752; (C) CM 46749; (D) CM 46769. Scale bar = 5 mm.

Nasal.—The sickle-shaped nasal bears both rostral and lateral processes. The rostral process is long, slender, and directed anteriorly, whereas the lateral process is shorter, broader, and directed anterolaterally. The posterior margin of the nasal is rounded.

Premaxilla.—The pars dentalis of the premaxilla (Fig. 4A, B) is edentulous. The alary process has a triangular shape in anterior aspect. A small process (CM 46707) located on the anterior surface of the lateral side of the premaxilla seems to articulate with the anterior notch of the maxilla. The pars palatina (CM 46714) of the premaxilla lacks a palatine process, and is narrow medially and broad laterally where it articulates with the pars palatina of the maxilla.

Maxilla.—The maxilla (Fig. 4E, F) is edentate. The notched anterior end (anterior notch) is expanded dorsally, forming the pars facialis (CM 46706, 46769). The maxilla is very slender posterior to the pars facialis. The pars palatina of the maxilla (CM 46707, 46753) originates directly posterior to the level of the anterior notch and extends posteriorly. Anterior and palatine processes are absent.

Quadratojugal.—The quadratojugal has not been identified in any specimen of *Chelomophrynus bayi.*

Parasphenoid.—The cultriform process of the parasphenoid tapers to a point anteriorly. Posterior to the cultriform process, the parasphenoid broadens laterally to form the corpus which lacks lateral alae. The length and shape of the corpus vary (Fig. 5) from tapering somewhat abruptly into the cultriform process (CM 46753) to tapering very gradually (CM 46772). Posterior lateral expansions (as defined by Cannatella, 1985) are present, but small (CM 46753). The posterior margin is notched.

Vomer.—The vomer is found in only two specimens, CM 46710 (Fig. 6A) and 46754, in which it is not in articulation with adjacent elements thereby making its orientation uncertain. However, because it is similar in overall shape to the vomer of *Scaphiopus,* the orientation of the *C. bayi* vomer is based on that which occurs in *Scaphiopus.* The anterior process of the *C. bayi* vomer is shorter than the posterior process, which lacks teeth. A medial flange of bone, which occurs in *R. dorsalis* (Fig. 6B), is absent. The postchoanal ramus is elongate and oriented somewhat anteriorly.

Palatine.—A palatine has not been identified. It is probably absent in *Chelomophrynus bayi* as it is in *Rhinophrynus dorsalis* (Trueb and Cannatella, 1982).

Pterygoid.—The pterygoid has not been positively identified. In CM 44488 the right mandible and upper maxillary arch are crushed together. Located at the posterior end of these bones is a sliver of bone that is either a fragment of the mandible or is the pterygoid.

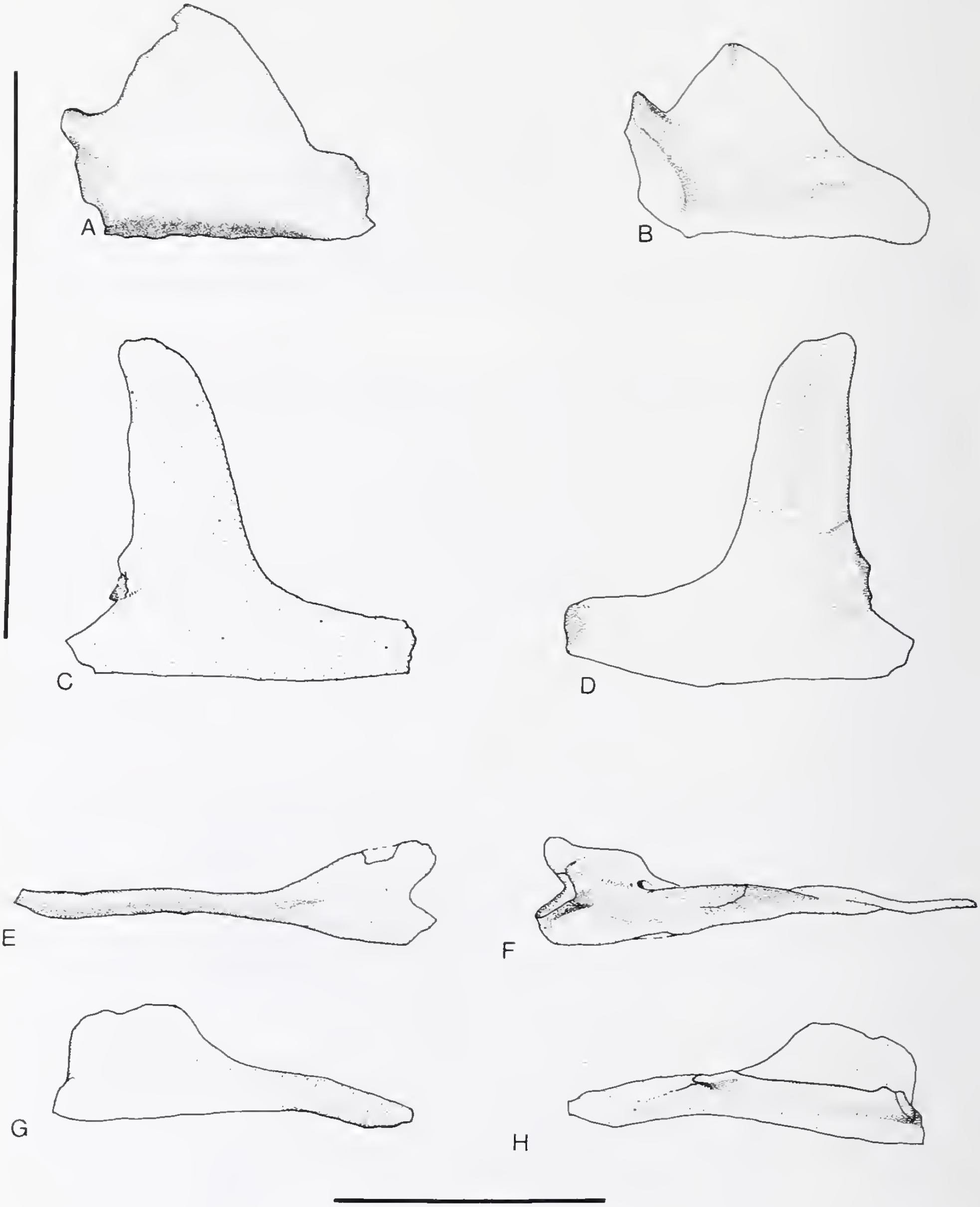


Fig. 4.—Premaxilla (A–D) and maxilla (E–H) of *Chelomophrynus bayi* and *Rhinophrynus dorsalis.* (A) *C. bayi,* CM 46707, right in anterior view; (B) *C. bayi,* CM 46714, right in posterior view; (C) *R. dorsalis,* KU 84883, right in anterior view; (D) *R. dorsalis,* KU 84883, right in posterior view; (E) *C. bayi,* CM 44496, right in lateral view; (F) *C. bayi,* CM 46753, right in medial view; (G) *R. dorsalis,* MSU 2295, left in lateral view; (H) *R. dorsalis,* MSU 2295, left in medial view. Scale bars = 5 mm.

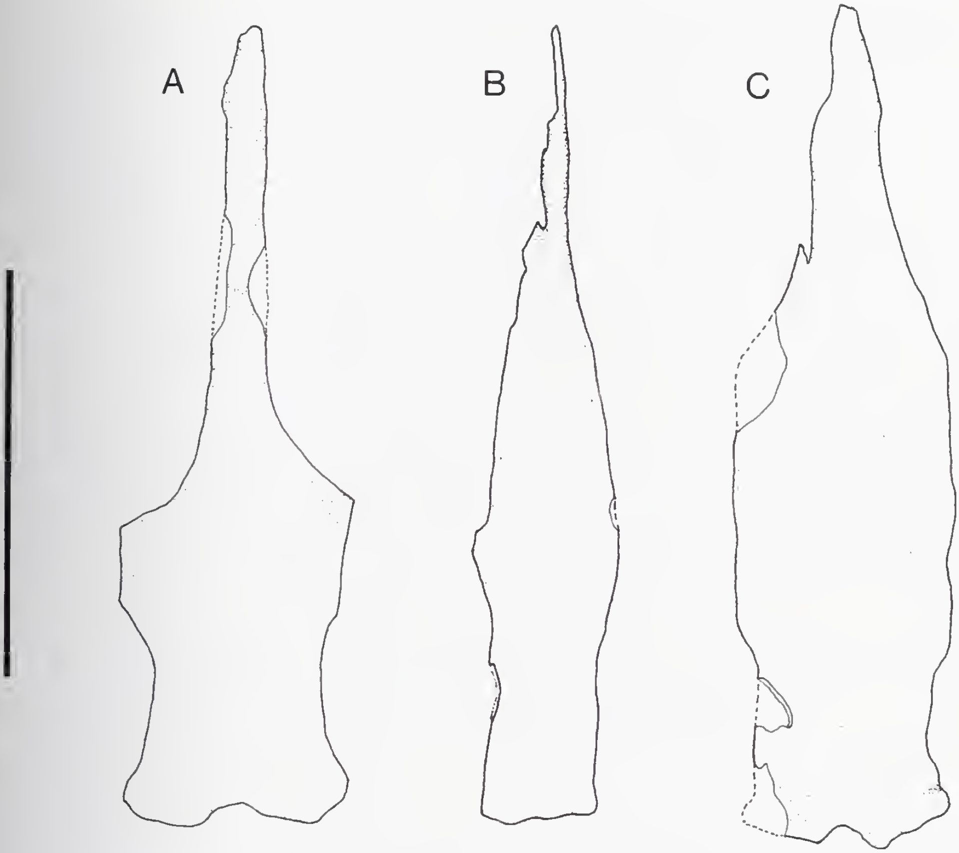


Fig. 5.—Variation in parasphenoid shape of *Chelomophrynus bayi.* (A) CM 46753; (B) CM 46771; (C) CM 46772. Scale bar = 5 mm.

Squamosal.—The squamosal (Fig. 6C) is exposed only in CM 44488, in which it is uncrushed and visible in lateral aspect. It consists of a broad ventral ramus and a small zygomatic ramus, which extends anteriorly 0.5 mm from the anterodorsal edge of the ventral ramus. The posterodorsal surface is covered by bone, so it cannot be certainly determined if an otic ramus is present; however, a thin ridge of bone on the dorsolateral edge of the ventral ramus may represent the lateral edge of the otic ramus. This ramus in *R. dorsalis* (Fig. 6D) is dorsolaterally oriented and articulates with the ventrolateral edge of the anterior part of the crista parotica.

Sphenethmoid.—The rostral process of the sphenethmoid is rounded. Right and left lateral processes, located approximately one-third of the length of the element from the anterior end, are directed anterolaterally. At the base of the lateral processes the sphenethmoid narrows medially. The orbitonasal foramen, located on the lateral wall of the sphenethmoid at the base of the lateral process, is surrounded by bone (CM 46742). The dorsolateral edge of the posterior end of the sphenethmoid is curved (CM 46742); this curvature may represent the anterodorsal border of the optic-prootic foramen, as in *Rhinophrynus dorsalis* (Trueb and Cannatella, 1982).

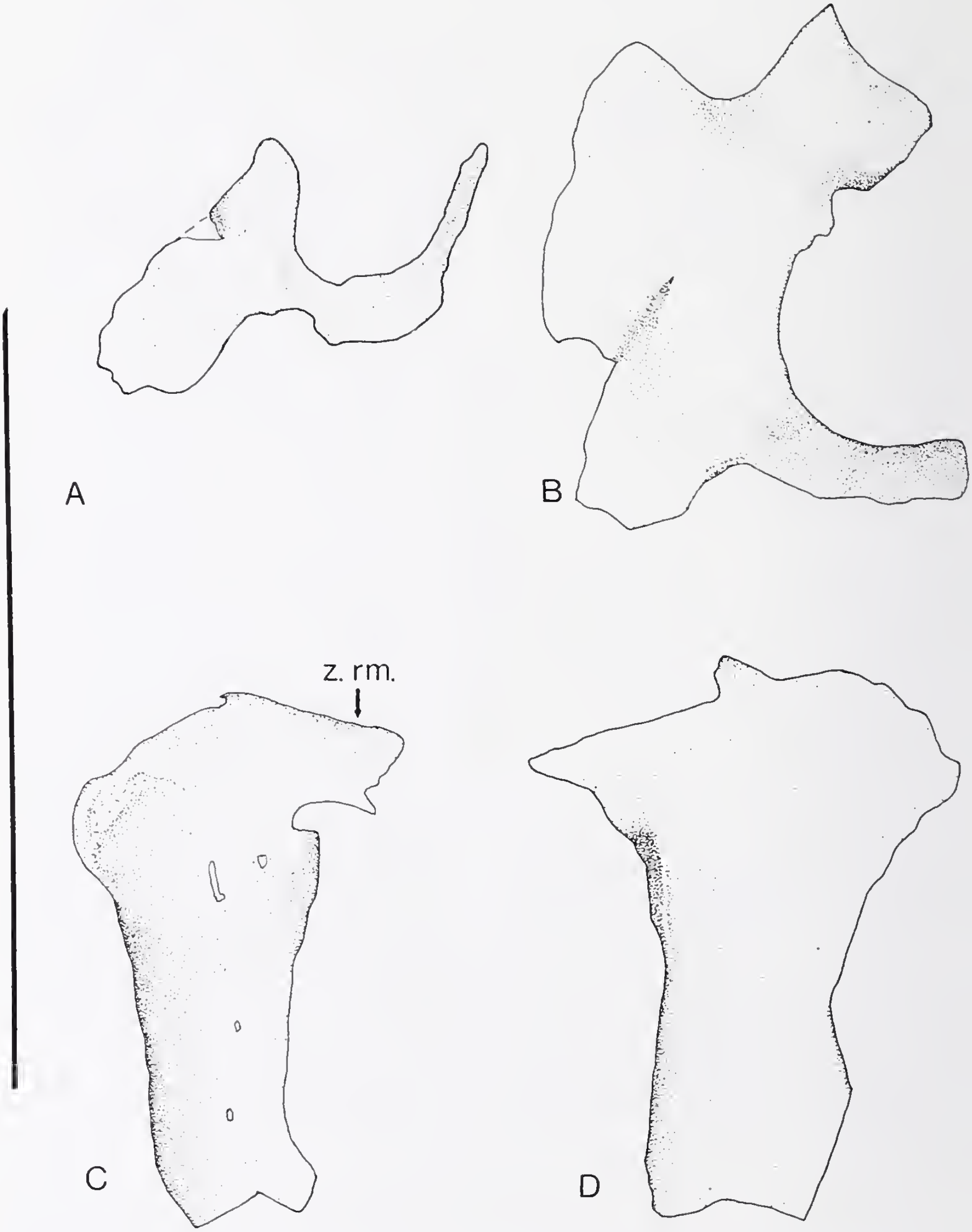


Fig. 6.—Vomer (A, B) and squamosal (C, D) of *Chelomophrynus bayi* and *Rhinophrynus dorsalis.* (A) *C. bayi,* CM 46710, right in ventral view; (B) *R. dorsalis,* KU 84885, right in ventral view; (C) *C. bayi,* CM 44488, right in lateral view; (D) *R. dorsalis,* MSU 2256, right in lateral view. Abbreviation: z.rm., zygomatic ramus. Scale bar = 5 mm.

Exoccipital-prootic complex.—The exoccipital and prootic are indistinguishably fused, a condition which occurs in most anurans (Trueb, 1973). Henceforth, these two bones will be called the exoccipital-prootic complex. The prootic region is roughly diamond-shaped in dorsal view, bears a lateral, rectangular process (crista parotica), and houses the otic capsule. Description of foramina piercing the otic capsule is based on CM 46712, although they can also be seen, in part, in CM 44496 and CM 46701. In CM 46712 (Fig. 2) the exoccipital-prootic complex is split through the foramen magnum, exposing the anteromedial and posteromedial walls of the right otic capsule. The anterior and posterior acoustic foramina pierce the posterior end of the anteromedial wall of the otic capsule. A thin, vertically-oriented, bony pillar separates the anterior and posterior acoustic foramina. The dorsal endolymphatic foramen pierces the anteromedial wall of the otic capsule directly dorsal to the acoustic foramina. The superior and inferior lymphatic foramina lie on the posteromedial wall of the otic capsule. Again, as in the acoustic foramina, a thin, vertically-oriented bony pillar separates the lymphatic foramina. A thick, vertically-oriented pillar of bone separates the acoustic foramina from the lymphatic foramina. The anteromedial edge of the prootic is concave; this concavity probably forms the posterior, posterodorsal, and posteroventral walls of the optic-prootic foramen, as in *Rhinophrynus dorsalis* (Trueb and Cannatella, 1982). The fenestra ovalis (CM 46707, 46775, 46776), the size of which cannot be determined due to crushing, faces posterolaterally.

The paired exoccipitals, which are fused medially, form the posterior portion of the braincase. The occipital condyles are closely juxtaposed. The jugular foramen lies lateral and slightly ventral to each condyle.

Quadrate.—An ossified quadrate has not been identified. It is likely that the mandible articulated with the skull via a cartilaginous quadrate.

Lower jaw

Dentary.—The dentaries are edentate and visible only in CM 46706, in which the left dentary is completely exposed and the right is partly covered. The left dentary is elongate and tapers at the anterior and posterior ends, both of which are rounded. The lateral surface is convex and the medial surface is concave. Ossified mentomeckelian bones have not been identified.

Angulosplenial.—The robust angulosplenial is preserved in many specimens; this description is based on CM 44496, in which it is preserved in lateral view, and CM 46724, in which it is preserved in medial view. The posterior end of the element is deep, but at its midlength the bone begins to taper dorsoventrally to a point at the anterior end. The element is curved medially, the coronoid process is not well developed, and the medial surface is trough-like.

Hyoid apparatus

Hyoid.—In Recent frogs, the hyoid can contain three bony elements: the parahyoid bone and the paired posteromedial processes of the hyoid. These elements have been identified in *Chelomophrynus bayi,* although only in CM 46781 (Fig. 7A). Here, the anteromedial surface of the parahyoid bone is partly covered by the skull. The two laterally-directed rami of the parahyoid bone are broad where they meet medially and taper to a point laterally. A third posteriorly-projecting process is short and somewhat broad. Due to overlying bone it is impossible to determine whether another short process extends anteriorly from the posterior process, as in *Rhinophrynus dorsalis.* The paired posteromedial processes are

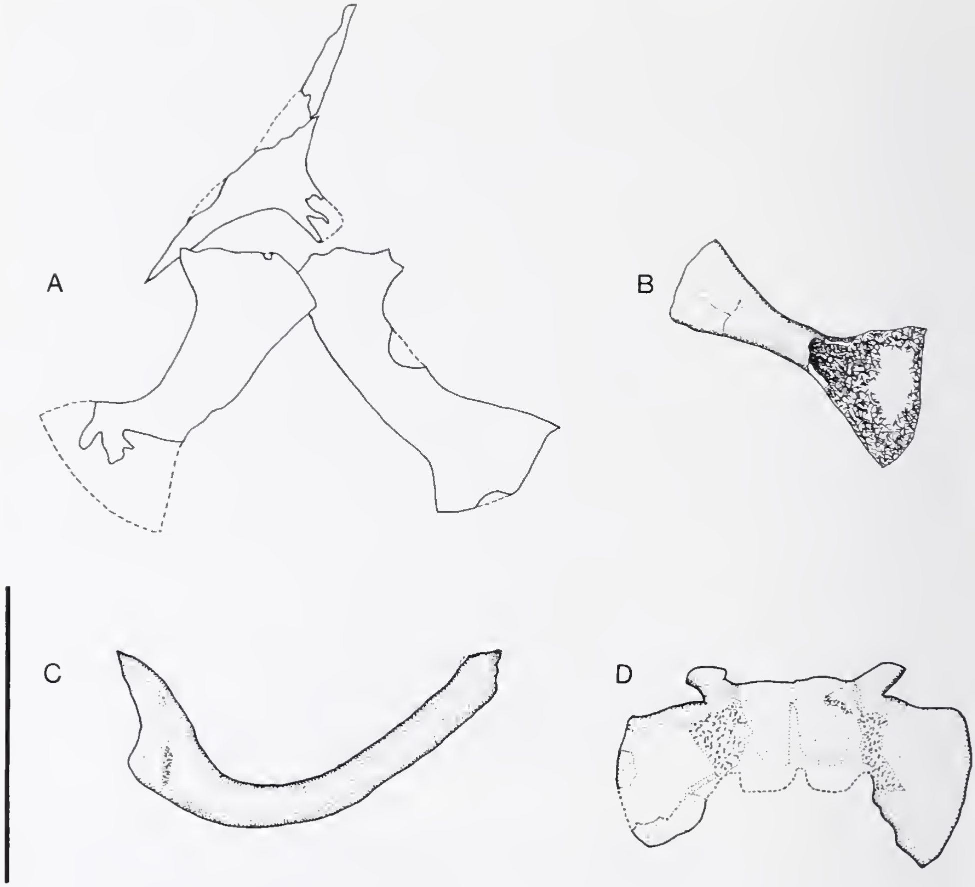


Fig. 7.—*Chelomophrynus bayi.* (A) Parahyoid bone and paired posteromedial processes, as preserved in CM 46781; (B) coracoid, CM 46716, right in ventral view; (C) clavicle, CM 46721, right in ventral view; (D) sacral vertebra, CM 46764, ventral view. Scale bar = 5 mm.

relatively robust. Their anterior and posterior ends are expanded, and the shaft is broad and dorsoventrally flattened.

Postcranial skeleton

Clavicle.—The clavicle (Fig. 7C) is strongly curved which indicates that the pectoral girdle of *Chelomophrynus bayi* is arciferal. It has a broad articular surface on the posterior edge of the lateral end, indicating that it most probably overlapped the scapula anteriorly. The medial end is narrow.

Suprascapula.—The suprascapula was not identified in *Chelomophrynus bayi.* It probably was not ossified, a condition that occurs in most anurans (Trueb, 1973).

Scapula.—The description of the scapula is based on CM 46716. Here, it is relatively long and the ventral end is cleft, having both a pars acromialis and pars glenoidalis. The anterior edge of the scapula is straight, whereas the posterior edge is concave. The widths of the dorsal and ventral ends are subequal. The ventral end of the anterior margin bears an articulating surface for the clavicle.

Coracoid.—Both ends of the coracoid (Fig. 7B) are expanded. The medial end is approximately twice as wide as the lateral end.

Cleithrum.—The medial end of the cleithrum is forked, forming anterior and posterior processes. The anterior process is approximately twice as long as the posterior process. The anterior process joins the anterior edge of the main body at an angle of approximately 130° in adults; this angle is somewhat greater in tadpoles. A ridge extends along the anterodorsal surface. The posterior margin is paper thin and relatively straight.

Humerus.—In anterior and posterior aspects, the proximal and distal ends of the humerus meet at an angle of approximately 147°, a condition that will be called strongly angulated. The well-developed crista ventralis, located on the ventral surface of the proximal half of the shaft (CM 46712), bears a small crest on its medial surface (CM 46754). The distal ball is bounded by two epicondyles, one each on the medial and lateral sides. The medial epicondyle is the larger of the two, and its medial surface is triangular (CM 44496). The lateral epicondyle is small (CM 46762). A ridge extends from the crista ventralis to the medial epicondyle (CM 46712). The medial crest, dorsal to the aforementioned ridge, extends from the medial epicondyle to the shaft. On the lateral side, the lateral crest is relatively long and moderately well developed; it joins the shaft at the same level as the medial crest (CM 44488). The raised triangular olecranon scar is situated medially on the dorsal surface of the distal end (CM 46763).

Radioulna.—The proximal end of the radioulna, which bears a well-developed olecranon process (CM 44485), is narrower than the distal end. The longitudinal sulcus is restricted to the proximal and distal ends in larger specimens and extends the length of the shaft in smaller specimens.

Manus.—Where preserved, the bones of the manus are disarticulated and extremely scattered. Thus it is impossible to determine the phalangeal formula or identify the individual elements.

Atlas.—The atlas is exposed in dorsal and dorsolateral views in many of the specimens, although it is crushed and broken in most. The neural arch is elongated in all specimens examined and almost completely overlaps the neural arch of the second vertebra, when found in articulation with it (CM 46722, 46749). The neural spine, which extends from the anterior to posterior margins of the neural arch, is present in some, but not all atlases. It is thin and low in CM 44496, broad and low in CM 46714, and well developed in CM 46711. The posterior end of the neural arch is broken away in CM 46712 (Fig. 2), but a swelling is present at the anterior end of the neural arch, suggesting that a neural spine was present. CM 44483 and 46722 lack a neural spine. A groove, situated where the neural spine would be located, occurs in CM 44481 and CM 46749. The neural arch, in dorsal view, tapers posteriorly from the level of the posterior zygapophysis. The posterior margin of the neural arch is irregular whereas the posterolateral margins are either smooth (CM 44483, 46722) or irregular (CM 46714, 46749).

Presacral vertebrae.—The eight, imbricate, amphicoelous, and ectochordal presacral vertebrae (Fig. 2, 12, 13, 14) have elongated transverse processes on the second through fourth vertebrae; those of the third vertebra are the longest (CM 46706). The distal end of the transverse process on the second vertebra is oriented anteriorly, forming a hook (CM 46712, 46722, Fig. 2, 13). The transverse processes on the fourth through eighth vertebrae are short and laterally oriented (CM 46706). There are no free ribs.

Sacral vertebra.—The sacral vertebra bears two condyles posteriorly (CM 46764, Fig. 7D). The sacral diapophyses are expanded anteroposteriorly, but most of the expansion is posterior. The neural arch is notched posteriorly which is best exemplified in the vertebral series of CM 46712 (Fig. 2), in which postmortem rotation of the sacral vertebra has brought its posterior end anterior.

Urostyle.—In most specimens having a urostyle, it is crushed and preserved in lateral view (Fig. 2). The bone is relatively robust and lacks vestigial transverse processes. A dorsal crest runs from the anterior end almost to the posterior tip.

Ilium.—The shaft of the ilium is slightly curved, laterally keeled, and lacks ridges. A well-developed, variably-shaped, triangular dorsal prominence arises from the dorsal acetabular expansion (CM 46712). The apex of the dorsal prominence is rounded in six specimens and pointed in two. The anterior margin is longer than the posterior margin in four specimens, shorter in three, and subequal in one. This variation occurs in some specimens of similar size. Thus, it is believed that the observed variation is not the result of growth. The dorsal prominence is always wider than high. The junction of the shaft with the ventral acetabular expansion is more excavated than that of the dorsal acetabular expansion. The ilial portion of the acetabulum, preserved in only a few specimens (CM 46716, 46728), is higher than wide and projects laterally from the acetabular expansion, the ventral lip of the cup more so than the dorsal lip. The ilial junction is V-shaped (CM 44486).

Ischium.—The paired ischia are fused medially (CM 44486). CM 46716 is the only specimen in which the ischial portion of the acetabulum is preserved and here the width is greater than the height, and the posterodorsal lip projects more strongly laterally than the ventral lip.

Femur.—The shaft of the femur is slightly bowed medially. The distal end is dorsoventrally flattened and bears lateral and medial condyles. The larger lateral condyle extends from the distal end of the femur to the posterior side of the shaft, so as to be posterolaterally oriented. In smaller specimens the lateral condyle is wider than long, but this is most likely the result of crushing. The length and width of the lateral condyle are subequal in the large, uncrushed specimen (CM 46761). In this femur, the shaft flares out to meet the lateral condyle and is expanded proximal to the condyle. The medial condyle is small in large femora and absent in femora of younger individuals. The shaft bears two crests, the lateral and medial crests (CM 46716, 46714). Because it is found in the same position, the lateral crest is believed to be homologous to the single, femoral crest (crista femoralis of Špinar, 1972) that occurs in many other anurans.

Tibiofibula.—The tibiofibula, shorter than the femur (Table 2), has the overall shape of an hourglass, with proximal and distal ends subequal in width. The medial surface of the proximal end is concave and the lateral surface convex. The dorsal edge of the proximal end is rounded, whereas the ventral edge forms a ridge. The medial surface of the distal end is smooth, but, unfortunately, the lateral distal surface is not well preserved in any specimen examined. A distinct longitudinal sulcus extends the length of the bone in smaller specimens, but becomes less apparent in larger older specimens, and is restricted to the proximal and distal ends.

Tarsus.—The proximal series consists of a tibiale and fibulare (Fig. 8). The tibiale is, on the average, 1.4 mm shorter than the fibulare. Proximal and distal ends of the tibiale are expanded. Its lateral side is strongly concave and longer than the medial side, which is slightly concave. The proximal and distal ends of the fibulare are expanded; the lateral side is slightly concave and longer than the strongly concave medial side. Proximal and distal ends of the tibiale and fibulare

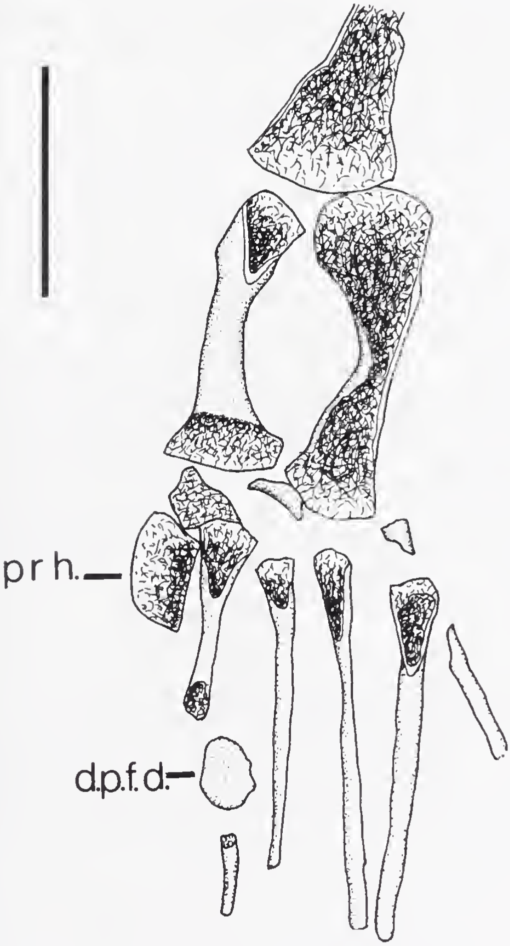


Fig. 8.—Left hind foot of *Chelomophrynus bayi* as preserved in CM 46756. Abbreviations: d.p.f.d., distal phalanx of first digit; prh., prehallux. Scale bar = 5 mm.

are fused in larger specimens (Stage VI: CM 46712, 46755) and unfused in smaller specimens (stages I–V). In specimens where they are fused, the space between the two bones forms a proximodistally-oriented oval (CM 46755).

The hindfoot is best seen in CM 46756 (Fig. 8). Here, the centrale lies distal to the tibiale and is positioned proximal to, and slightly between, the prehallux and first metatarsal. Tarsals 2 and 3, which are fused, lie distal to the point at which the tibiale and fibulare meet. There are five metatarsals. The prehallux is modified as a digging spade. A smaller spade is closely associated with the first digit and most likely is a modified distal phalanx of this digit, as in *Rhinophrynus dorsalis.* The phalangeal formula cannot be determined because the phalanges are either not preserved or widely scattered.

Rhinophrynus Duméril and Bibron, 1841

Type species.—Rhinophrynus dorsalis Duméril and Bibron, 1841.

Revised diagnosis.—Rhinophrynus is distinguished from *Eorhinophrynus* and

Chelomophrynus by lateral crest of humerus poorly developed, shaft of femur strongly bowed and narrow directly proximal to distal condyle, distal condyle of femur longer than wide.

Rhinophrynus dorsalis Duméril and Bibron, 1841

Holotype.—MNHNP 693.

Revised diagnosis.—*Rhinophrynus dorsalis* is distinguished from *R. canadensis* by dorsal prominence of ilium poorly developed, and space between tibiale and fibulare forming mediolaterally elongate oval.

Rhinophrynus canadensis Holman, 1963

Holotype.—SMNH 1425, right ilium.

Referred material.—Holotype and SMNH P661.1907–P661.1915, tarsals; SMNH P661.1901, P661.1902, P661.1916–P661.1931, femora; SMNH P661.1905, P661.1906, P661.1951–P661.1971, ilia; SMNH P661.1903, humerus; SMNH P661.1947–P661.1950, radioulnae; and SMNH P661.1946, vertebra.

Horizon and locality.—Cypress Hills Formation, near Eastend, Saskatchewan, Canada, early Oligocene.

Revised diagnosis.—*Rhinophrynus canadensis* is distinguished from *R. dorsalis* by dorsal prominence of ilium well developed, and space between tibiale and fibulare forming proximodistally elongate oval.

ONTOGENY

Fossil tadpoles are relatively rare and generally poorly preserved; consequently, few have been described in any detail. *Shomronella jordanica* (Pipidae), represented by numerous tadpoles from the early Cretaceous of central Israel, was described in detail and staged by Estes et al. (1978) using normal tables for *Xenopus laevis* (Nieuwkoop and Faber, 1956). Nevo (1956) reported another early Cretaceous tadpole from south central Israel. In a redescription of the late Cretaceous *Saltenia ibanezi* (Pipidae), Báez (1981) reported the existence of several ontogenetic stages, including tadpoles, in a large collection of this frog from Argentina. Estes (1977) discussed several tadpoles of *Eoxenopides reuningi* (Pipidae) from Paleogene fissure fill deposits in South Africa and, following comparisons with *Xenopus laevis,* noted they were at late stages of metamorphosis. A large collection of palaeobatrachid and pelobatid tadpoles from the Miocene of Czechoslovakia was described and staged by Špinar (1972). Špinar devised his own staging scheme, finding comparisons with normal tables of *X. laevis* (Nieuwkoop and Faber, 1956) to be difficult. Piveteau (1955) reported on a tadpole of unknown affinity from the Miocene of Spain.

The Lysite Mountain collection contains a developmental series consisting of tadpoles undergoing metamorphosis, young adults and adults. Comparison of these tadpoles with the normal table for *X. laevis* (Nieuwkoop and Faber, 1956) is not possible, because the table stages are often defined on soft tissue characters. Trueb (1985) compared the timing of skull ossification (the appearance of skeletal elements) among various groups of anurans, including rhinophrynids. Her data for *R. dorsalis* could not be compared with those from *C. bayi* because there are no complete or articulated skulls in this collection. This makes it impossible to determine whether an element is absent because it had not ossified, or it floated away and was not preserved with the skull. Instead, the *C. bayi* collection was divided into six stages representing a growth series. The stages were based on landmarks in ossification such as the appearance of processes, condyles, and some skeletal elements. The latter feature was avoided when possible, because, as mentioned, it is difficult to demonstrate whether an element is truly absent or merely not preserved with the specimen. The relative stage of metamorphosis of the tadpoles was determined from comparison with cleared and stained tadpoles of *R. dorsalis* staged according to Gosner (1960, given as arabic numerals). The six stages recognized are described below.

In Stage I individuals (Fig. 9) the limb bones are small and lack condyles, the partes acromialis and glenoidalis on the scapula are not ossified, nor is the dorsal prominence on the ilium. This stage is roughly equivalent to Stage 42 which is characterized by the beginning of metamorphosis of the head region, the emergence of forelimbs, and the presence of a tail. In Stage II (Fig. 10) the pars acromialis of the scapula is ossified, the nasal bears only a rostral process, and the acetabulum on the ilium begins to form. By Stage III (Fig. 11) the lateral process is present on the nasal. Stages II and III fall between stages 42 and 44 during which metamorphosis of the head region continues. Stage IV (Fig. 12) is distinguished by the presence of both the partes acromialis and glenoidalis on the scapula, presence of the dorsal prominence, fusion of the radius and ulna, and fusion of the tibia and fibula. Stage IV is approximately equivalent to Stage 44 in which metamorphosis of the head region continues and the tail is resorbed to a stub. In Stage V (Fig. 13, 14), the condyles are ossifying on the limb bones, the sacral diapophyses are present, the urostyle is present, and the acetabulum is well formed. This stage represents transformed young adults; metamorphosis is complete. The specimens in this stage exhibit increasing size. The last stage, Stage VI (Fig. 2), is marked by fusion of the tibiale and fibulare at their ends and larger size of the specimens.

An ontogenetic description of each element and the first stage of occurrence is given below. Variation is discussed when appropriate. Table 3 lists specimens by stage and position in the growth series.

Skull

Frontoparietal.—An impression of a large, well-formed frontoparietal is found in the Stage I specimen CM 44491, the youngest specimen in the collection. The observed variation in shape of the frontoparietal (see description above, Fig. 3, and Table 2) is not the result of growth. For example, the Stage II specimens, CM 46752 and 44497, exhibit the endpoints for the range in robustness (CM 46752, 68.2; CM 44497, 90.6). Also, the rostrum of CM 46752 is longer and more pointed than that of CM 44497. The Stage III specimens, CM 46731 and 46749 show differences in shape in which the sides either form apparent angles (CM 46731), or are more rounded (CM 46749).

Nasal.—The nasal is first seen in Stage II (CM 46752, Fig. 15) where it is small and crescent-shaped, lacking a lateral process. Ossification of the lateral process proceeds first in a lateral and then an anterolateral direction. The lateral process is small and laterally-oriented at Stage III (CM 46749) and larger with an anterolateral orientation at Stage IV (CM 46704).

Premaxilla.—The youngest preserved premaxilla is in Stage IV (CM 46704, Fig. 12), in which it is thin and not well ossified. By Stage V (CM 46729) it is well developed.

Maxilla.—The maxilla is first noted in Stage IV (CM 46704, Fig. 12); it is poorly

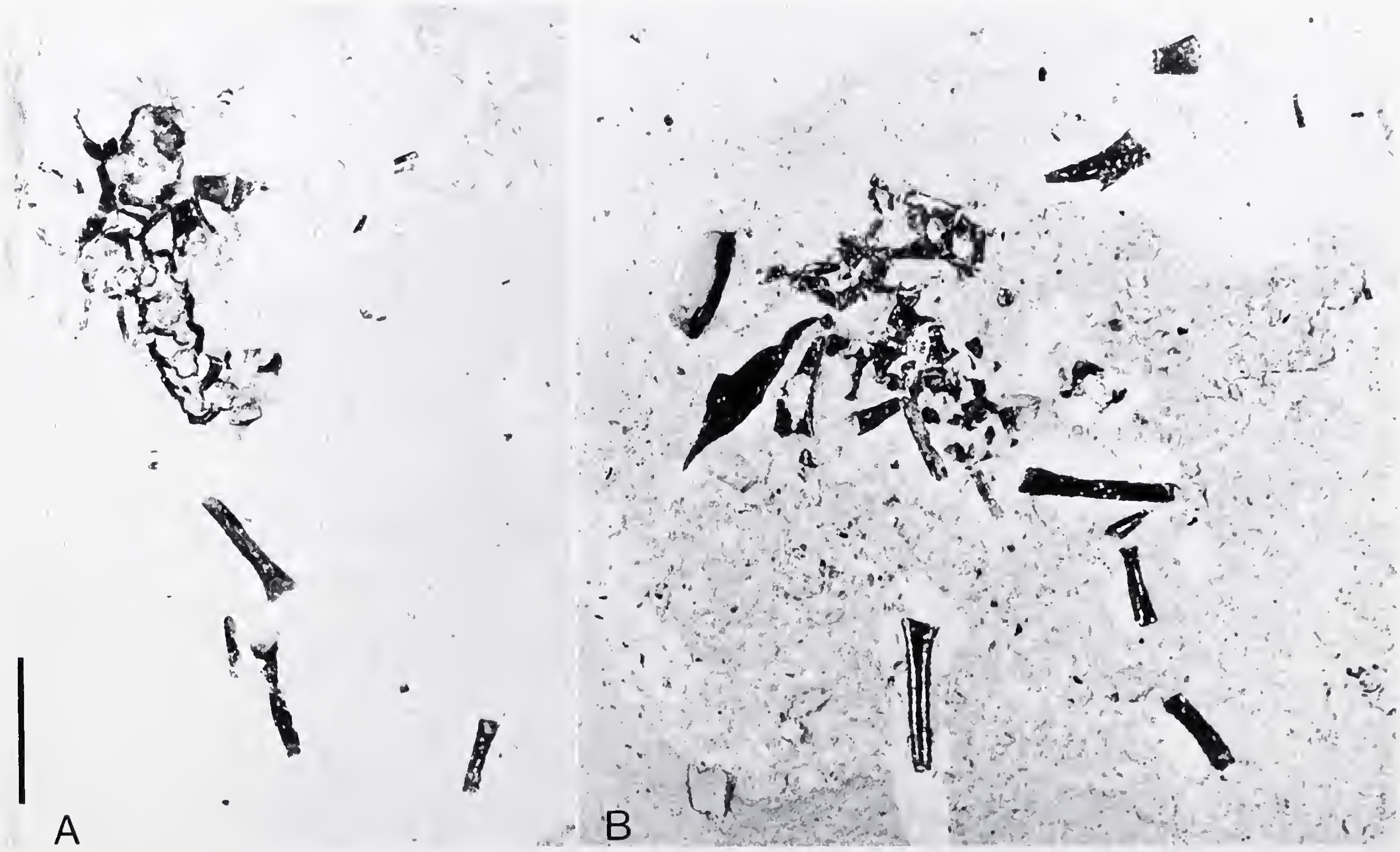


Fig. 9.—*Chelomophrynus bayi* at Stage I. (A) CM 44491; (B) CM 46725. Scale bar = 5 mm.

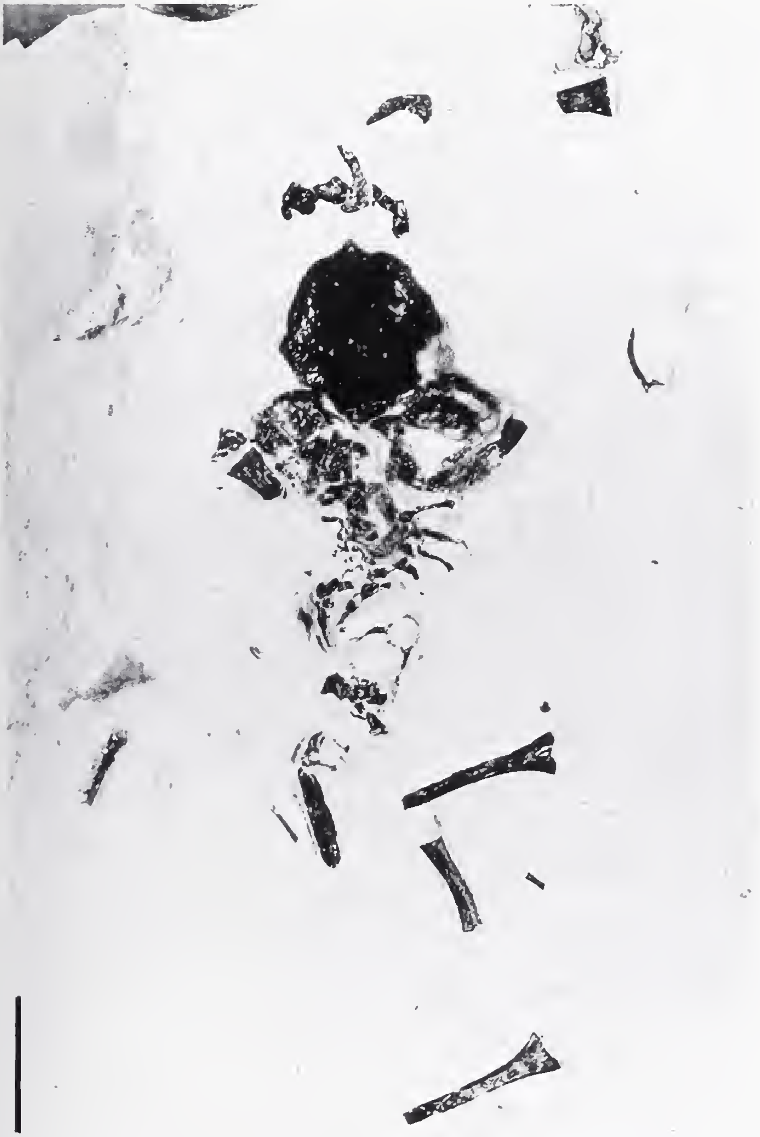


Fig. 10.—*Chelomophrynus bayi,* CM 44497, Stage II. Scale bar = 5 mm.

ossified and incomplete anteriorly because of breakage. The pars palatina is present. At Stage V, the maxilla (CM 46706) is well ossified and fully developed.

Parasphenoid.—This element is first found in the Stage I specimen CM 46725 (Fig. 9), in which it is the largest bone in the skeleton. Variation in the length and shape of the corpus (see description above and Fig. 5) is not the result of devel-

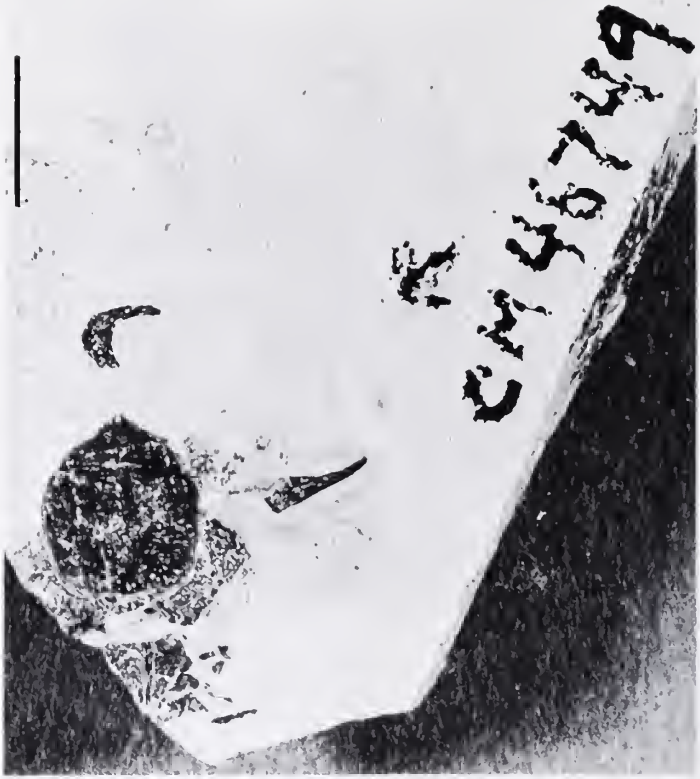


Fig. 11.—*Chelomophrynus bayi*, CM 46749, Stage III. Scale bar = 5 mm.

opment, evidence for which can be seen in parasphenoids from Stage V individuals (CM 46700, 46772).

Vomer.—The only two vomers identified occur in Stage V individuals.

Squamosal.—The squamosal is exposed only in the Stage V specimen CM 44488 in which it is well ossified.

Sphenethmoid.—A small trough-shaped bone in the Stage II specimen, CM 44497 (Fig. 10), may be the anterior end of the sphenethmoid. The lateral processes are not well developed in the smaller examples (CM 46736, Stage V, Fig. 16A; CM 46773, 46774, stage unknown), but become longer and more defined as ossification progresses (CM 46742, Stage V, Fig. 16B).

Exoccipital-prootic complex.—In Stage I (CM 46725) the exoccipital and prootic are fused and the occipital condyle and jugular foramen are present, but the crista parotica is not. The crista parotica begins to ossify by Stage IV (CM 46704, Fig. 12), and is well formed by Stage V (CM 46723).

Lower jaw

Dentary.—The dentaries are exposed only in CM 46706 (Stage V) in which they are well ossified.

Angulosplenial.—Two Stage II specimens, CM 44497 (Fig. 10) and CM 44482, have bones that may be angulosplenials, but positive identification of these ele-

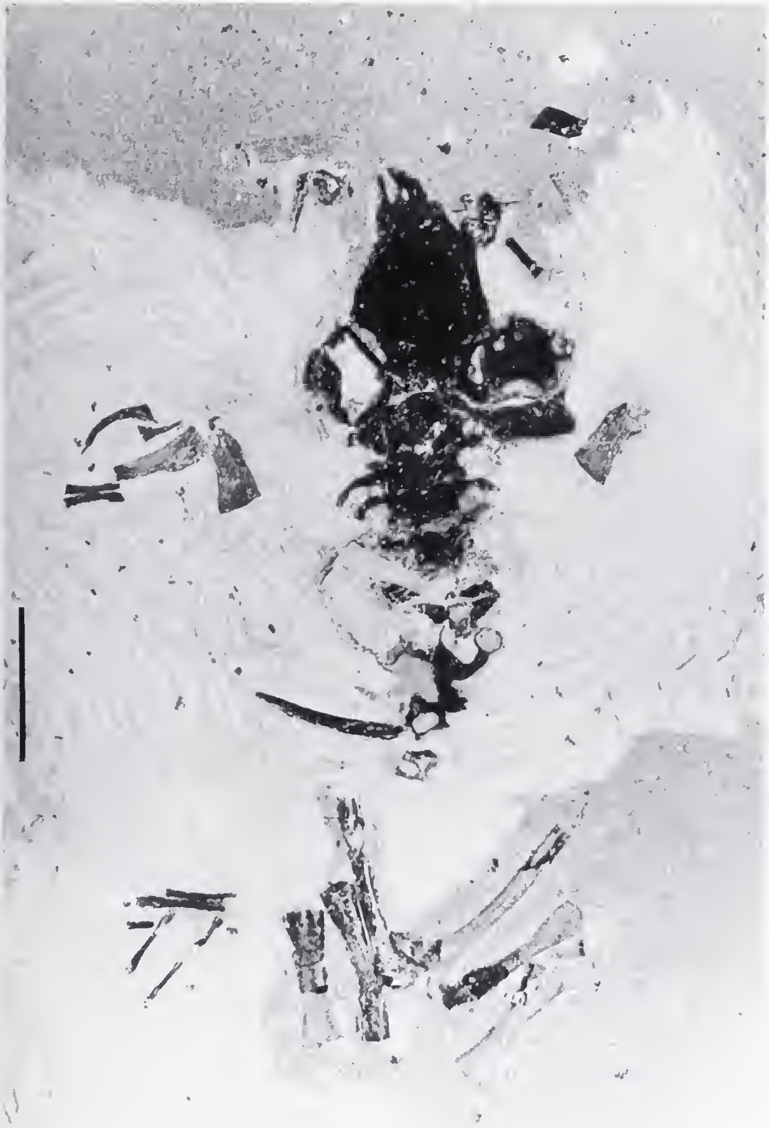


Fig. 12.—*Chelomophrynus bayi,* CM 46704, Stage IV. Scale bar = 5 mm.

ments has not been made due to the lack of diagnostic features. The angulosplenial ossifies in a posterior-to-anterior direction (Fig. 16C, D). Only the posterior half of the element is ossified in stages III (CM 44483) and IV (CM 46704). The entire bone is ossified by Stage V (CM 46734).

Postcranial skeleton

Clavicle.—The smallest clavicle, in CM 44497 (Fig. 10) at Stage II, resembles that from an older individual and differs only in size.

Scapula.—At Stage I (CM 44491, 46725), the partes acromialis and glenoidalis

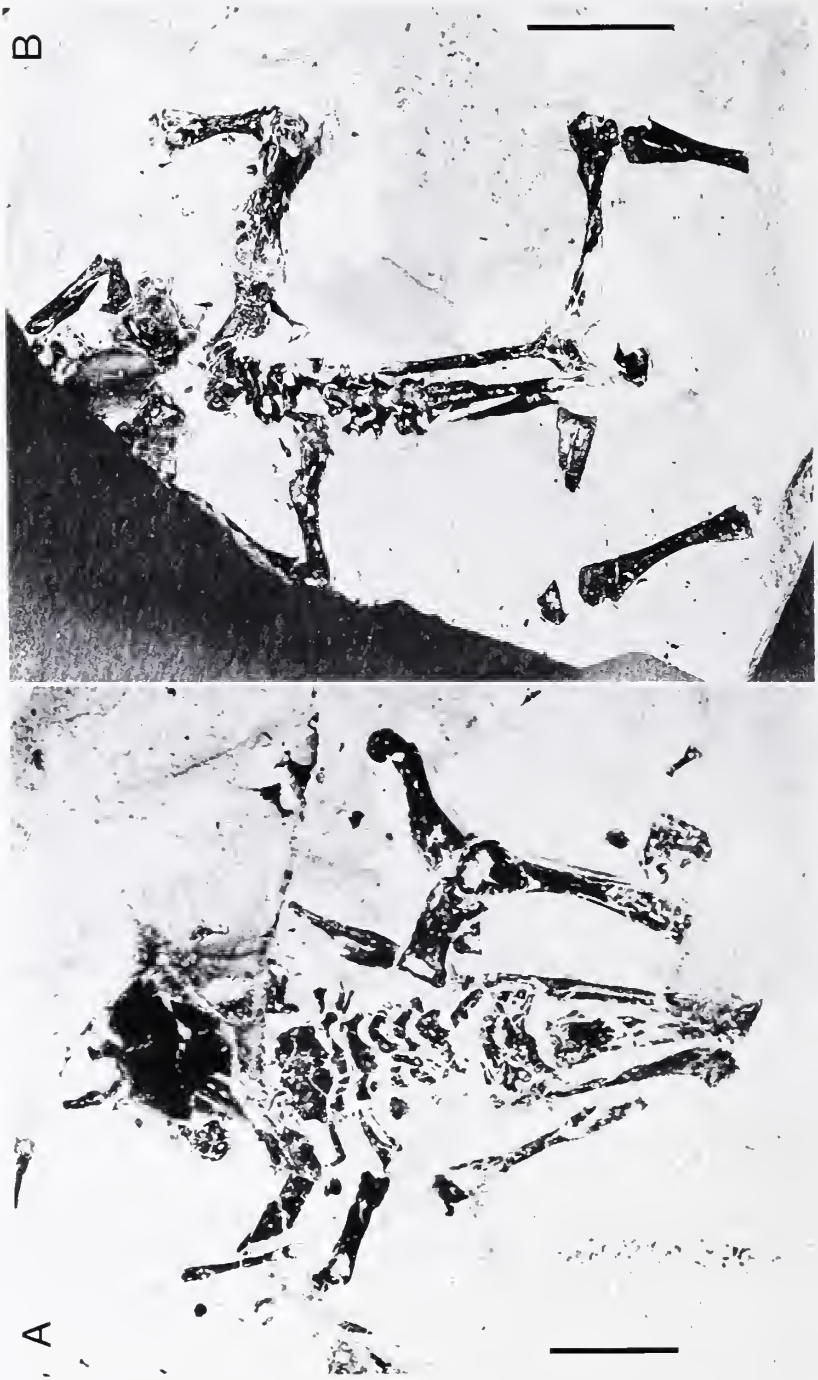


Fig. 13.—*Chelomophrynus bayi* at Stage V. (A) CM 46722; (B) 44488. Scale bars = 5 mm.

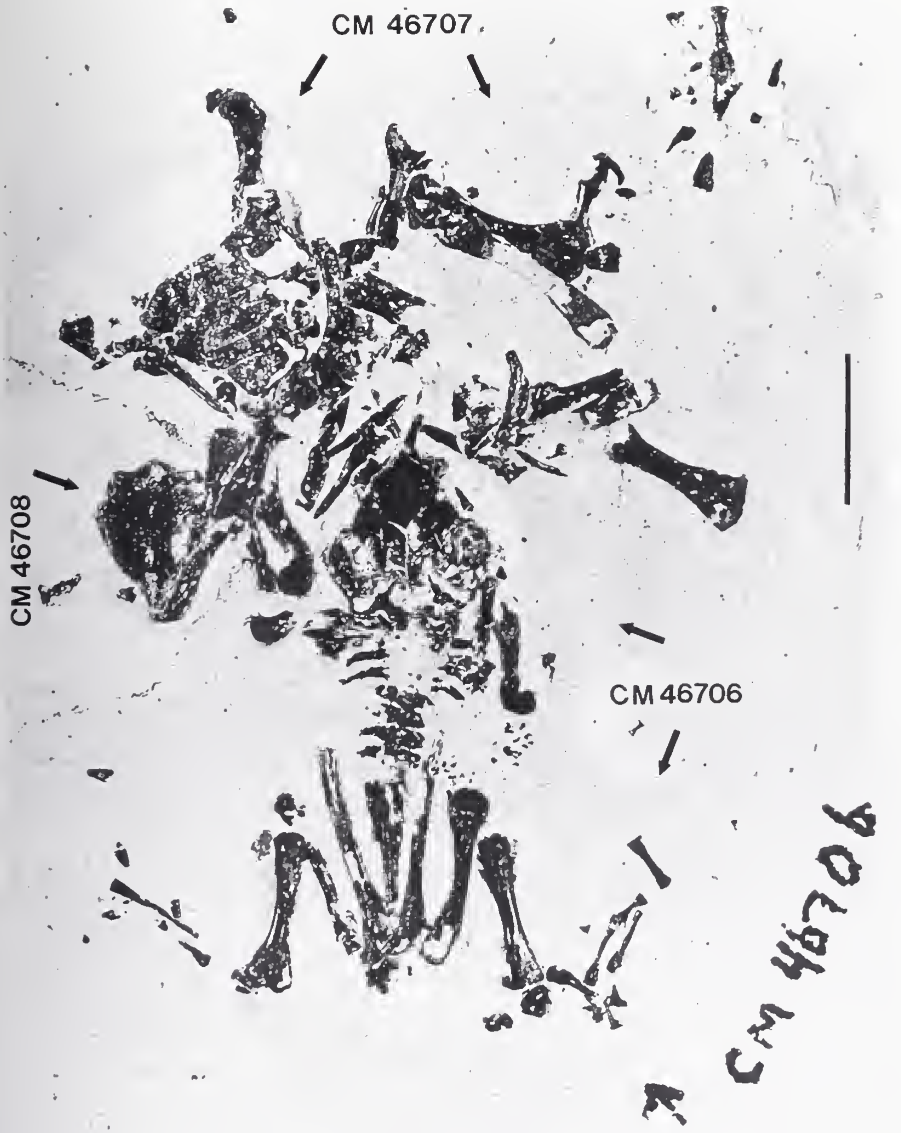


Fig. 14.—*Chelomophrynus bayi,* CM 46706, CM 46707, CM 46708, Stage V. Scale bar = 5 mm.

are unossified, and the dorsal end of the scapula is wider than the ventral (Fig. 17A–D). Stage II (CM 44497) shows the beginning of ossification of the pars acromialis as a small point on the medial surface of the ventral end of the scapula. The pars glenoidalis first occurs in Stage IV (CM 46704) in which it is very small. The partes acromialis and glenoidalis are distinct processes by Stage V (CM 46722). The dorsal and ventral ends of the scapula are approximately equal in width at Stage V (CM 46722).

Table 3.—*Specimen numbers arranged according to position in growth series.*

Stage I:	44491, 46725, 46746
Stage II:	46752, 44497, 46750, 46730
Stage III:	46749, 46731, 44482, 46733, 46783
Stage IV:	46735, 46726, 46704, 46745, 46744, 46781
Stage V:	46728, 46722, 46723, 46717, 44497, 46706, 46741, 44487, 46736, 46721, 46729, 46743, 46710, 46715, 46708, 46737, 46714, 46707, 44495, 46701, 44488, 46711, 46720, 46740, 46762, 46705, 46724, 46765, 46727, 46768, 46703, 44480, 44496, 46753, 46739, 46700, 46719, 44492, 44498, 46756, 44486, 44485, 46751, 46716, 44493, 44489, 46761
Stage VI:	46755, 46712

Coracoid.—The coracoid is first found in CM 46704 at Stage IV (Fig. 12). It resembles that of older individuals, differing only in size.

Cleithrum.—The cleithrum is present at Stage I (CM 46725) in which it bears anterior and posterior processes (Fig. 17E, F). The angle between the anterior process and the anterior edge is reduced as development progresses; otherwise, the bone only grows larger with development.

Humerus.—The shaft of the humerus ossifies before the distal and proximal ends. The humerus is first noted in Stage I (CM 44491) in which only the center of the shaft is ossified, including a small portion of the crista ventralis (Fig. 18A–C). At Stage IV (CM 46704) the shaft is longer and the crista ventralis is well developed. The distal and proximal ends are not ossified until Stage V (CM 46717).

Radioulna.—There are two small, separate bones that may be the radius and ulna in CM 44491 at Stage I (Fig. 9A). The radioulna is definitely present in the Stage IV CM 46704, in which the radius and ulna are just beginning to fuse along the midpoint of the shaft (Fig. 18D–E). The bones are completely fused by Stage V (CM 46706).

Manus.—First appearance of the manus is at Stage V (CM 46706).

Atlas.—The atlas is present at Stage I in CM 44491 (Fig. 9A), but it is poorly

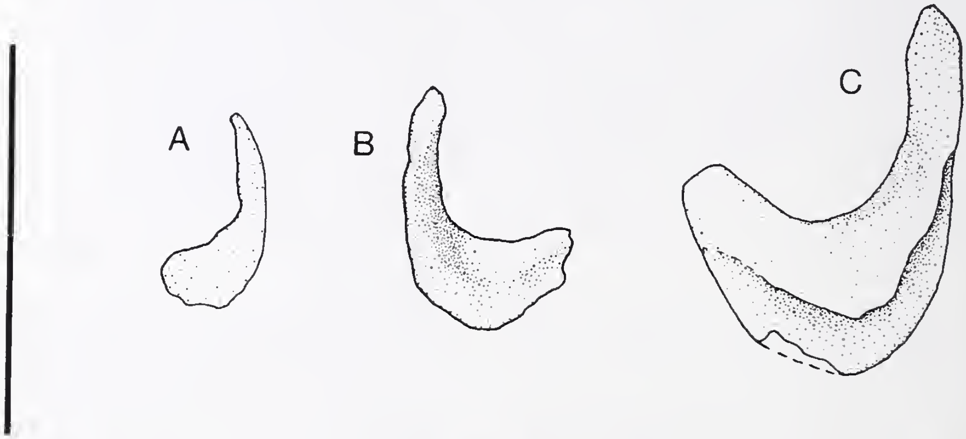


Fig. 15.—Growth series of nasal in *Chelomophrynus bayi.* (A) CM 46752, Stage I, left in dorsal view; (B) CM 46749, Stage III, right in dorsal view; (C) CM 46780, Stage V, left in dorsal view. Scale bar = 5 mm.

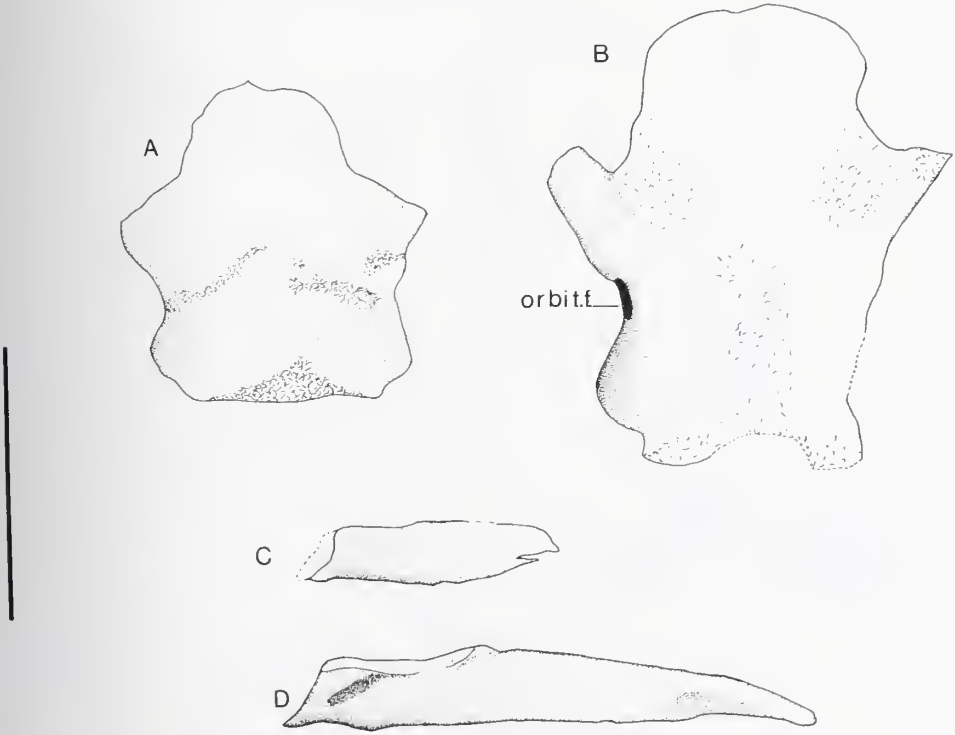


Fig. 16.—Growth series of sphenethmoid (A, B) and angulosplenial (C, D) in *Chelomophrynus bayi.* (A) CM 46736, Stage V, in ventral view; (B) CM 46742, Stage V, in ventral view; (C) CM 46704, Stage IV, left in medial view; (D) CM 46724, Stage V, left in medial view. Abbreviation: orbit.f., orbitonasal foramen. Scale bar = 5 mm.

preserved. The presence or absence of a neural spine may be related to development. Specimens between stages I and IV lack a neural spine (Stage I: CM 44480; Stage III: CM 44483, 46749, Fig. 11; Stage IV: CM 46704, Fig. 12), whereas those at stages V and VI may or may not have a spine (spine absent: CM 46722, Stage V, Fig. 13A; spine present: CM 44496, 46711, Stage V, and CM 46712, Stage VI, Fig. 2). CM 46722 is a small representative of Stage V and is the only specimen in this stage that lacks a spine. Possibly the spine would have developed in CM 46722 had this individual survived. Alternatively, the presence of a neural spine on the atlas may be a variable feature in *C. bayi.*

Presacral vertebrae.—These vertebrae ossify early in the development of *C. bayi* as seen in Stage I (CM 44491, Fig. 9A) where the neural arches are ossified and fused to the centra. The neural spines are the last portions of the vertebrae to ossify. They are poorly developed and short at Stage V (CM 46722, Fig. 13A), whereas at Stage VI (CM 46712, the largest individual collected, Fig. 2) they are considerably longer.

Sacral vertebra.—The sacral vertebra becomes larger and the sacral diapophyses more expanded during development. The sacral vertebra is present in Stage III (CM 44482) and Stage IV (CM 46704, Fig. 12), but the sacral diapophyses are not ossified. The youngest specimen having ossified sacral diapophyses is CM 46722 at Stage V (Fig. 13A).

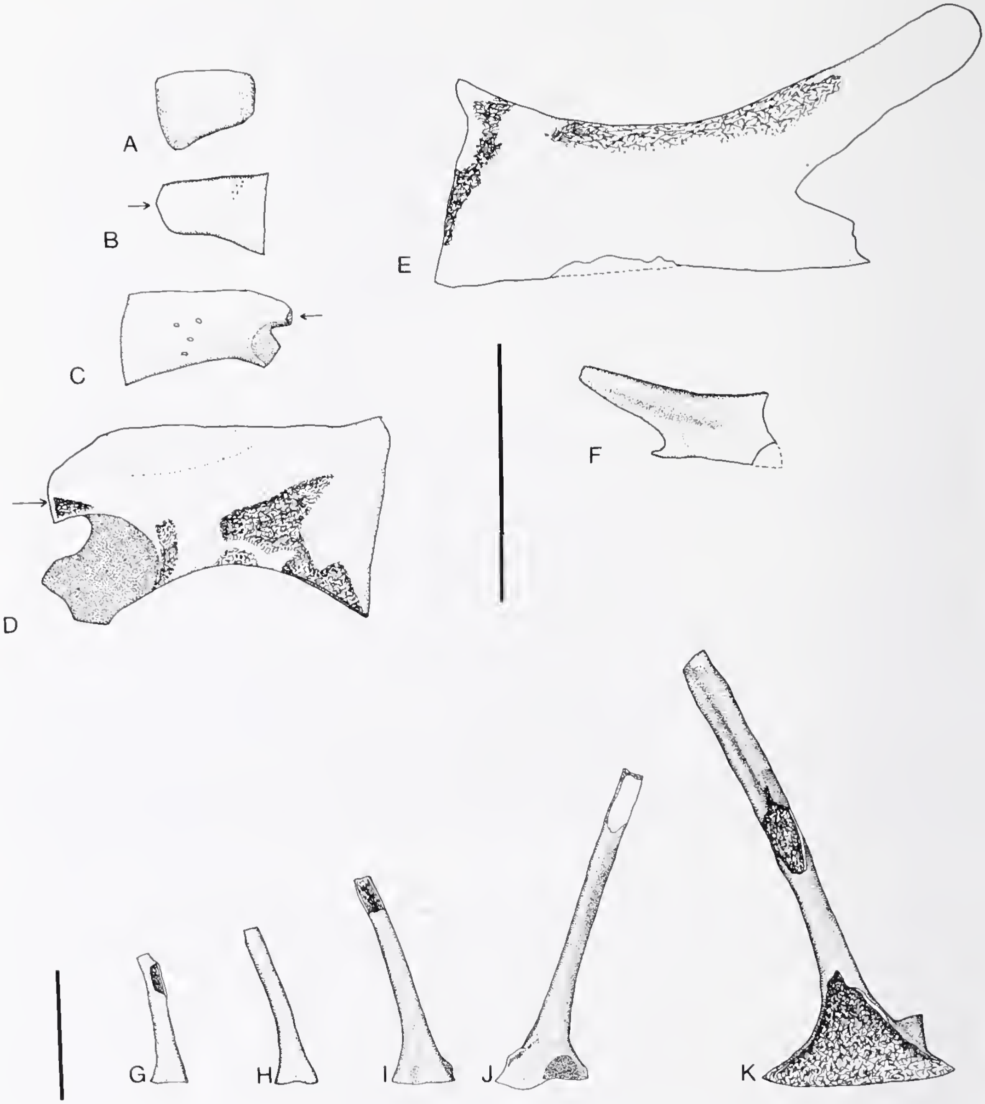


Fig. 17.—Growth series of scapula (A–D, arrow indicates pars acromialis), cleithrum (E, F), and ilium (G–K) in *Chelomophrynus bayi.* (A) CM 46725, Stage I, right in lateral view; (B) CM 44497, Stage II, left in lateral view; (C) CM 46704, Stage IV, right in lateral view; (D) CM 46716, Stage V, left in lateral view; (E) CM 46725, Stage I, right in dorsal view; (F) CM 46778, Stage V, left in dorsal view; (G) CM 44491, Stage I, right in medial view; (H) CM 44497, Stage II, right in medial view; (I) CM 46745, Stage IV, right in medial view; (J) CM 46728, Stage V, right in lateral view; (K) CM 46768, Stage V, left in lateral view. Scale bars = 5 mm.

Urostyle.—The urostyle is first apparent in Stage V (CM 46722, Fig. 13A) in which it has ossified anterior cotyles and a dorsal crest.

Ilium.—At Stage I (CM 44491, the youngest specimen), the shaft of the ilium is short, and the distal end is laterally flattened and slightly expanded dorsoventrally (Fig. 17G–K). Development of the acetabulum commences in Stage II (CM

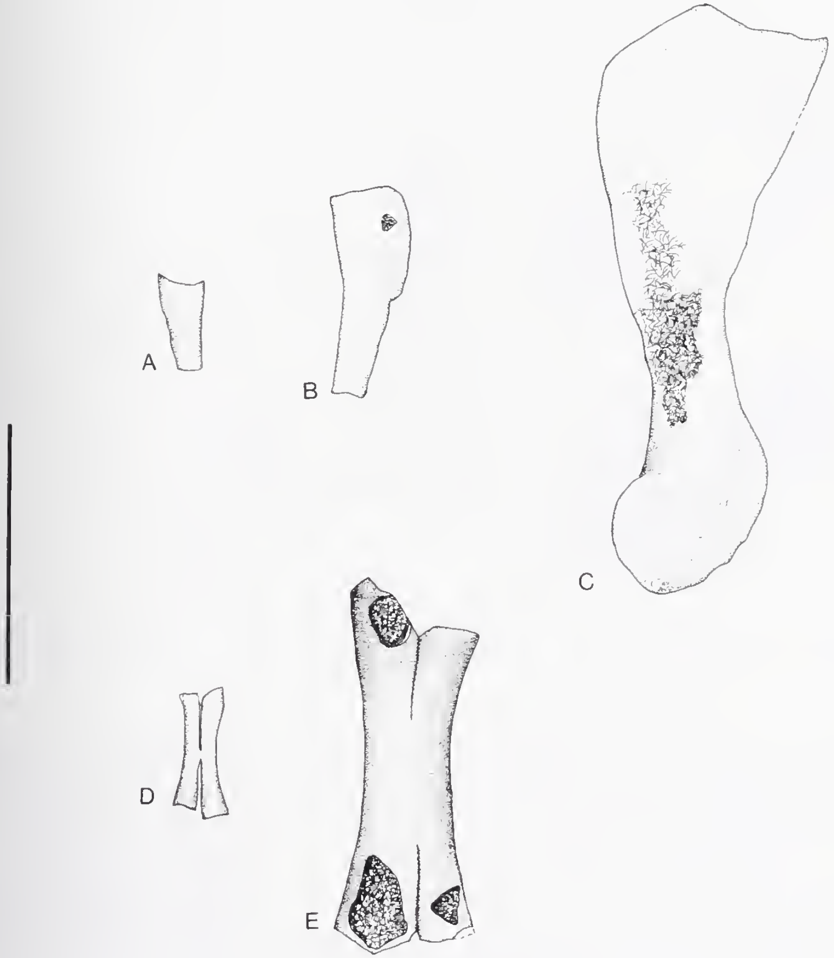
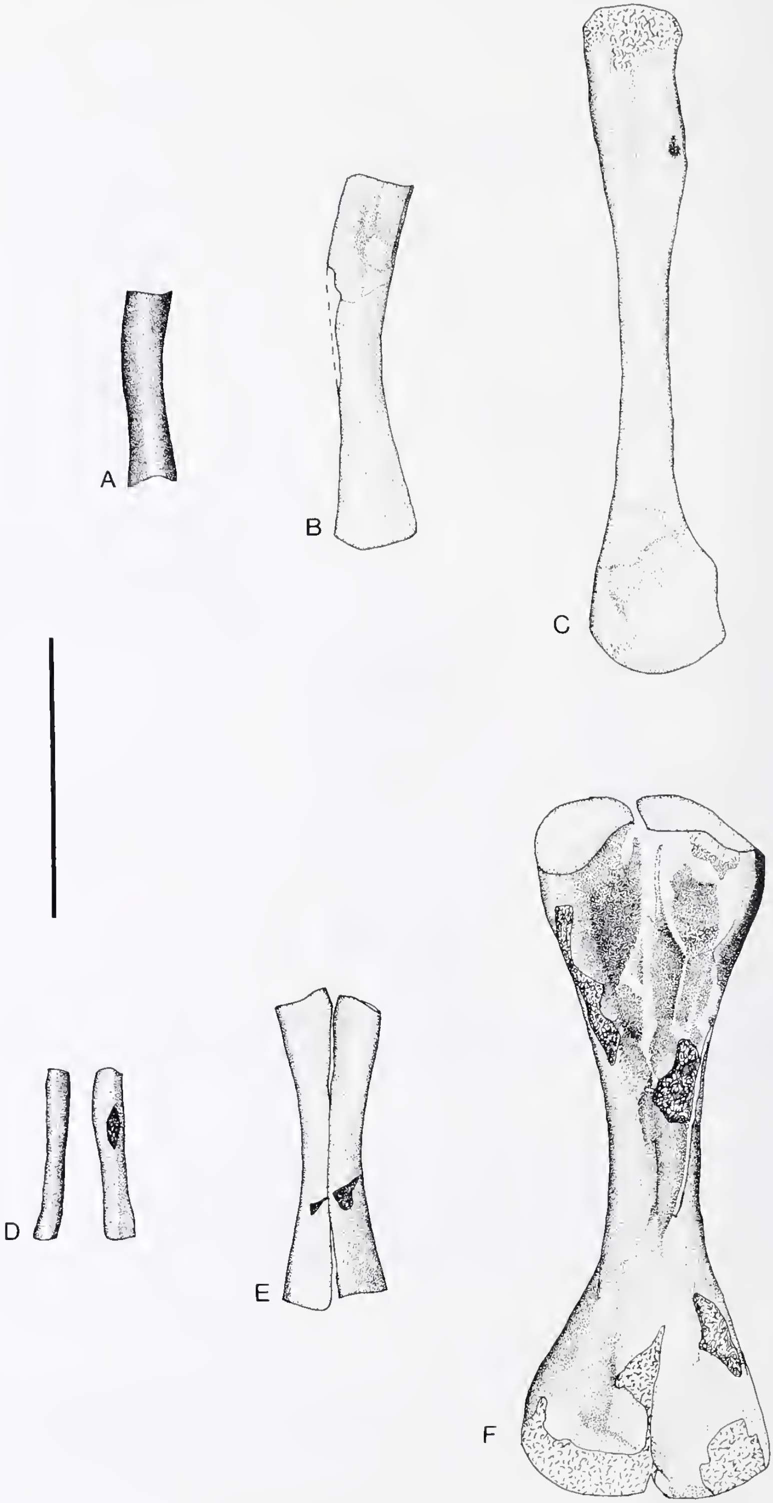


Fig. 18.—Growth series of humerus (A–C) and radioulna (D–E) in *Chelomophrynus bayi.* (A) CM 46725, Stage I, left in ventrolateral view; (B) CM 46704, Stage IV, left in medial view; (C) CM 46762, Stage V, left in lateral view; (D) CM 46704, Stage IV, left in anterior view; (E) CM 44485, Stage V, right in anterior view. Scale bar = 5 mm.

44497), as shown by invagination of the distal border and formation of the anterior acetabular lip (CM 46750). This area is filled with roughened bone in Stage IV (CM 46726), and the acetabulum is well formed in Stage V (CM 46728). The dorsal prominence is present as a small bump at Stage IV (CM 46745) and is well formed at Stage V (CM 46722). The junction of the shaft with the ventral acetabular expansion becomes more excavated concomitant with an increase in depth of the ventral acetabular expansion.

Ischium.—The smallest specimen with a preserved ischium is CM 44488 at Stage V (Fig. 13B). It is preserved in medial view causing the acetabulum to be hidden. The acetabulum most likely begins to form at Stage II, the same time as in the ilium.

Femur.—The shaft of the femur (Fig. 19A–C) ossifies before the distal condyles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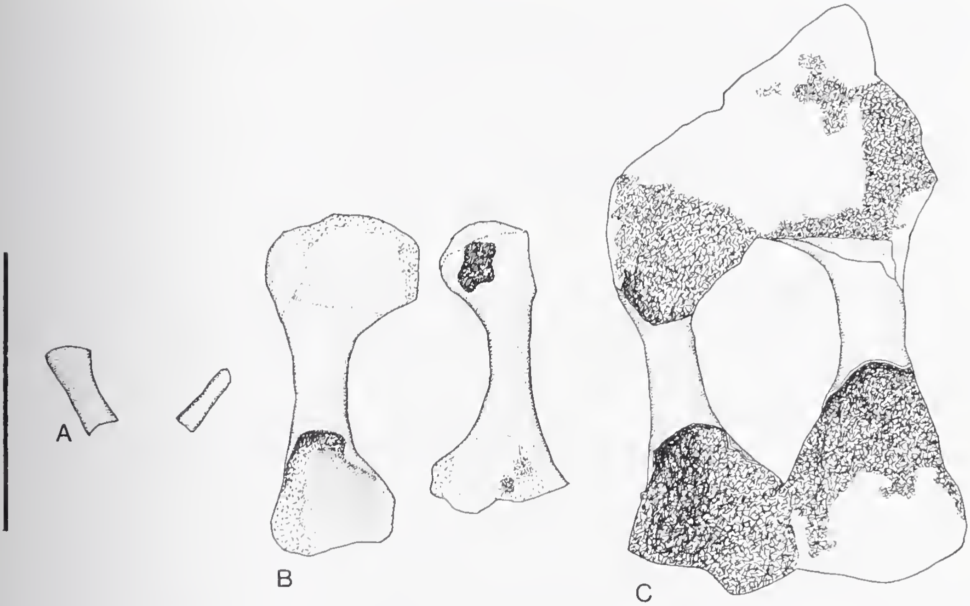

Fig. 20.—Growth series of tibiale and fibulare in *Chelomophrynus bayi.* (A) CM 46750, Stage II, right in dorsal view; (B) CM 46727, Stage V, left in ventral view; (C) CM 46755, Stage VI, left in dorsal view. Scale bar = 5 mm.

and the crests. Only the shaft is present in the smallest femur, CM 44491 at Stage I. In Stage III (CM 46733), Stage IV (CM 46704), and Stage V (CM 46728), the distal end is expanded. The lateral condyle begins to ossify at Stage V (CM 46722). The medial condyle (CM 46714, 46761) and crests (CM 46721) are present at Stage V, but their occurrence in smaller femora is difficult to determine due to crushing and limited exposure.

Tibiofibula.—The tibia and fibula are first found in Stage II (CM 46750) in which they are unfused (Fig. 19D–F). They are fused in Stage IV (CM 46704), but the proximal and distal ends are free. In CM 46765, at Stage V, only the extreme ends are free, and they are completely fused in CM 46739, a larger specimen at Stage V.

Hindfoot.—Aside from increasing in size, the tibiale and fibulare fuse at the proximal and distal ends (Fig. 20). Fusion is seen only in CM 46712 and 46755 at Stage VI, the oldest individuals. Toe bones are first noted in Stage II (CM 44497, Fig. 10).

CHARACTER ANALYSIS

Outgroup comparison was utilized to determine polarity for the 17 characters analyzed in this study (following the methods of Wiley, 1981, and Eldridge and

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Fig. 19.—Growth series of femur (A–C) and tibiofibula (D–F) in *Chelomophrynus bayi.* (A) CM 46750, Stage II, right in lateral view; (B) CM 46704, Stage IV, left in medial view; (C) CM 46714, Stage V, right in ventral view; (D) CM 46750, Stage II, right in lateral view; (E) CM 46704, Stage IV, right in medial view; (F) CM 46765, Stage V, left in medial view. Scale bar = 5 mm.

Cracraft, 1980). The outgroup consists of *Discoglossus pictus* (Discoglossidae), *Pelobates cultripes, Scaphiopus couchi,* and *S. bombifrons* (Pelobatidae). The above-mentioned pelobatids are suitable for the outgroup because they are members of the Pelobatoidea, which is considered the sister group to the Pipoidea (Cannatella and Trueb, 1988). *Discoglossus* is suitable because it is placed outside of the Mesobatrachia and Neobatrachia (Cannatella, 1985). Several characters used by Cannatella (1985) in his cladistic analysis of primitive frogs (archaeobatrachians) were included in this study as they are useful for determining the relationships among rhinophrynids.

1. *Alary process of premaxilla.*—The alary process of the premaxilla is triangular in *C. bayi* (Fig. 4A–D). A narrow, rectangular alary process is found in the outgroups and *R. dorsalis.* Therefore, a narrow, rectangular alary process is considered the primitive state, whereas a triangular alary process is considered the derived state.

2. *Anterior notch of maxilla.*—*C. bayi* possesses a notch on the anterior end of the maxilla (Fig. 4E–H). It is incipient to absent in the outgroups and *R. dorsalis.* Lack of an anterior notch is, therefore, considered the primitive state and possession the derived state.

3. *Medial flange of vomer.*—A medial flange of bone is present on the vomer of *R. dorsalis* (Fig. 6A, B). It is absent in the outgroups and *C. bayi.* Absence of a medial flange on the vomer is considered primitive and its presence derived.

4. *Length of anterior and posterior processes of vomer.*—In the outgroups and *R. dorsalis,* the anterior process of the vomer is longer than the posterior process (Fig. 6A, B). The posterior process is longer than the anterior process in *C. bayi.* The primitive state is considered to be an anterior process with greater length than the posterior process and the derived state is a posterior process with greater length than the anterior process.

5. *Postchoanal ramus of vomer.*—Cannatella (1985) observed that the postchoanal ramus, when present in primitive frogs, was elongate only in the genus *Scaphiopus.* He considered this condition to be derived and a short postchoanal ramus to be primitive. *Chelomophrynus bayi* has the derived condition whereas *D. pictus* and *R. dorsalis* have the primitive state (Fig. 6A, B). *Pelobates* does not have a postchoanal ramus.

6. *Zygomatic ramus of squamosal.*—The zygomatic ramus of the squamosal is present in all extant frogs except *R. dorsalis* (Trueb and Cannatella, 1982) and *Pipa* (Cannatella, 1985). It is present in *C. bayi* (Fig. 6C, D). The primitive state is considered to be the presence of a zygomatic ramus whereas the derived state is its absence (Cannatella, 1985).

7. *Orbitonasal foramen.*—Cannatella (1985) noted that in all anuran taxa except *R. dorsalis* the orbitonasal foramen pierces the lateral wall of the sphenethmoid in an anterior position, and considered this the primitive condition. In *R. dorsalis* the orbitonasal foramen is positioned more posteriorly, which is the derived state (Cannatella, 1985). *Chelomophrynus bayi* has the less-derived state in which the orbitonasal foramen is medially positioned (Fig. 16B).

8. *Fusion of cleithrum and suprascapula.*—Among extant anuran taxa, the cleithrum is fused to the suprascapula only in *R. dorsalis* (Trueb, 1973). It is not fused in *C. bayi* or the outgroups. Therefore an unfused cleithrum and suprascapula is considered the primitive state and fusion the derived state.

9. *Transverse process of posterior presacral vertebrae.*—Cannatella (1985) has considered laterally-oriented transverse processes on the last three posterior pre-

sacral vertebrae as the primitive state and anteriorly-oriented transverse processes as the derived state. The outgroup anurans and *R. dorsalis* have anteriorly-oriented transverse processes whereas those of *C. bayi* are directed laterally (Fig. 13A, B). The only known vertebra of *R. canadensis,* which has laterally-oriented transverse processes, is a posterior one, based on the very short length of the transverse process. In *R. dorsalis* the fifth vertebra bears very short laterally-oriented transverse processes. It is impossible to determine whether the vertebra of *R. canadensis* is the fifth or one located more posteriorly. For this reason, the state in *R. canadensis* cannot be determined.

10. *Dorsal prominence of ilium.*—The dorsal prominence of the ilium is absent to poorly developed in the outgroups and *R. dorsalis.* Holman (1963) stated that the dorsal prominence in *R. canadensis* is not as high as in *R. dorsalis,* but reexamination shows the opposite to be true. It is well developed in *C. bayi* (Fig. 21D–F). It has been considered that an absent to poorly-developed (broad and low) dorsal prominence is the primitive state and a well-developed dorsal prominence is the derived state (Cannatella, 1985, and Cannatella and Trueb, 1988), a conclusion with which this outgroup analysis is consistent.

11. *Lateral crest of humerus.*—Among rhinophrynids the lateral crest of the humerus is long and somewhat broad in *Eorhinophrynus* sp., *E. septentrionalis,* and *C. bayi* (Fig. 22A–D). The lateral crest is short and extremely poorly developed in *R. canadensis* and *R. dorsalis.* Estes and Reig (1973) noted that humeral crests show probable variation due to sexual dimorphism, as the crest in males is longer. Examination of skeletons proves this to be true in some pelobatids in which the crest extends to the midpoint of the shaft in males. Therefore, only the humerus from female pelobatids was used to evaluate this character. The sex of the *D. pictus* skeleton examined is unknown so it was not included in the outgroup for analysis of this character. *Rhinophrynus dorsalis* does not show sexual dimorphism in this character. The crest size does not vary greatly in *C. bayi* suggesting it also does not exhibit sexual dimorphism in humeral crest size. *Pelobates cultripes, S. couchi,* and *S. bombifrons* have a long, somewhat broad lateral crest which is considered the primitive state. The derived state is a short, poorly-developed lateral crest.

12. *Shaft of femur.*—The shaft of the femur is slightly bowed medially in *P. cultripes, S. couchi, S. bombifrons,* and *C. bayi,* and strongly bowed in *R. canadensis* and *R. dorsalis.* In *D. pictus* the shaft has a sigmoid configuration. A slightly bowed shaft is considered the primitive state and a strongly bowed shaft the derived state.

13. *Distal condyle of femur.*—The distal condyle of the femur is poorly developed, and the width is greater than the length in the outgroups. In rhinophrynids it is divided into distinct lateral and medial condyles; the lateral condyle is larger. The length and width of the lateral condyle are subequal in *C. bayi,* but the length is greater in *R. canadensis* and *R. dorsalis* (Fig. 22E–G). A lateral condyle that is wider than long is considered the primitive state, subequal width and length the derived state, and length greater than width a more derived state.

14. *Shaft above distal condyle(s) of femur.*—The shaft is expanded proximal to the distal condyle(s) in the outgroups and *C. bayi.* It is narrow in *R. canadensis* and *R. dorsalis* (Fig. 22E–F). An expanded shaft proximal to the distal condyle(s) is considered the primitive state and a narrow shaft the derived state.

15. *Space between tibiale and fibulare.*—The space or open area between the tibiale and fibulare is a proximodistally elongated oval in the outgroups, *Eorhino-*

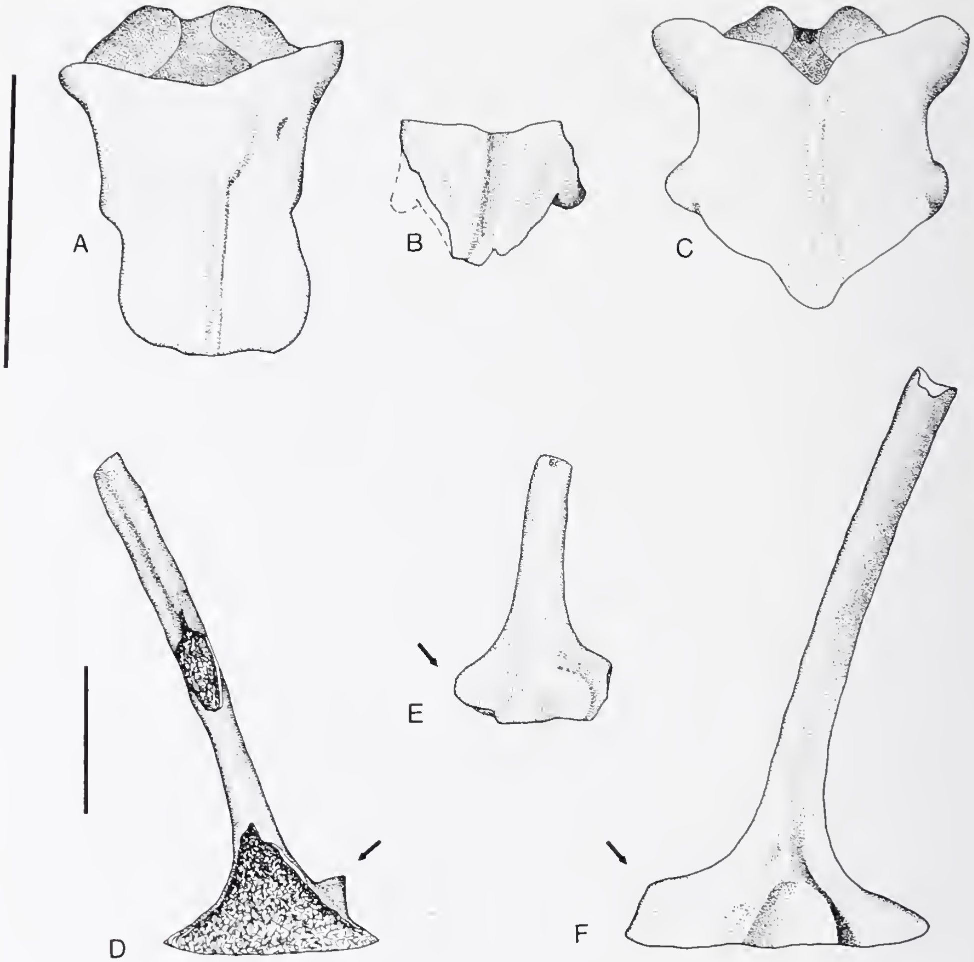

Fig. 21.—Comparison of atlas (A–C) and ilium (D–F, arrow indicates dorsal prominence) in *Chelomophrynus bayi, Eorhinophrynus septentrionalis,* and *Rhinophrynus.* (A) *E. septentrionalis,* AMNH 3818, dorsal view; (B) *C. bayi,* CM 46749, dorsal view; (C) *R. dorsalis,* UMMZ 152336, dorsal view; (D) *C. bayi,* CM 46768, left in lateral view; (E) *R. canadensis,* SMNH 1907, right in lateral view; (F) *R. dorsalis,* KU 152337, right in lateral view. Scale bars = 5 mm.

phrynus sp., *E. septentrionalis, C. bayi,* and *R. canadensis* (Fig. 23). It forms a mediolaterally elongate oval in *R. dorsalis.* A space with a proximodistally elongate oval is considered the primitive state, whereas a mediolaterally elongate oval is considered the derived state.

16. *Shape of atlantal neural arch.*—The atlantal neural arch tapers posteriorly

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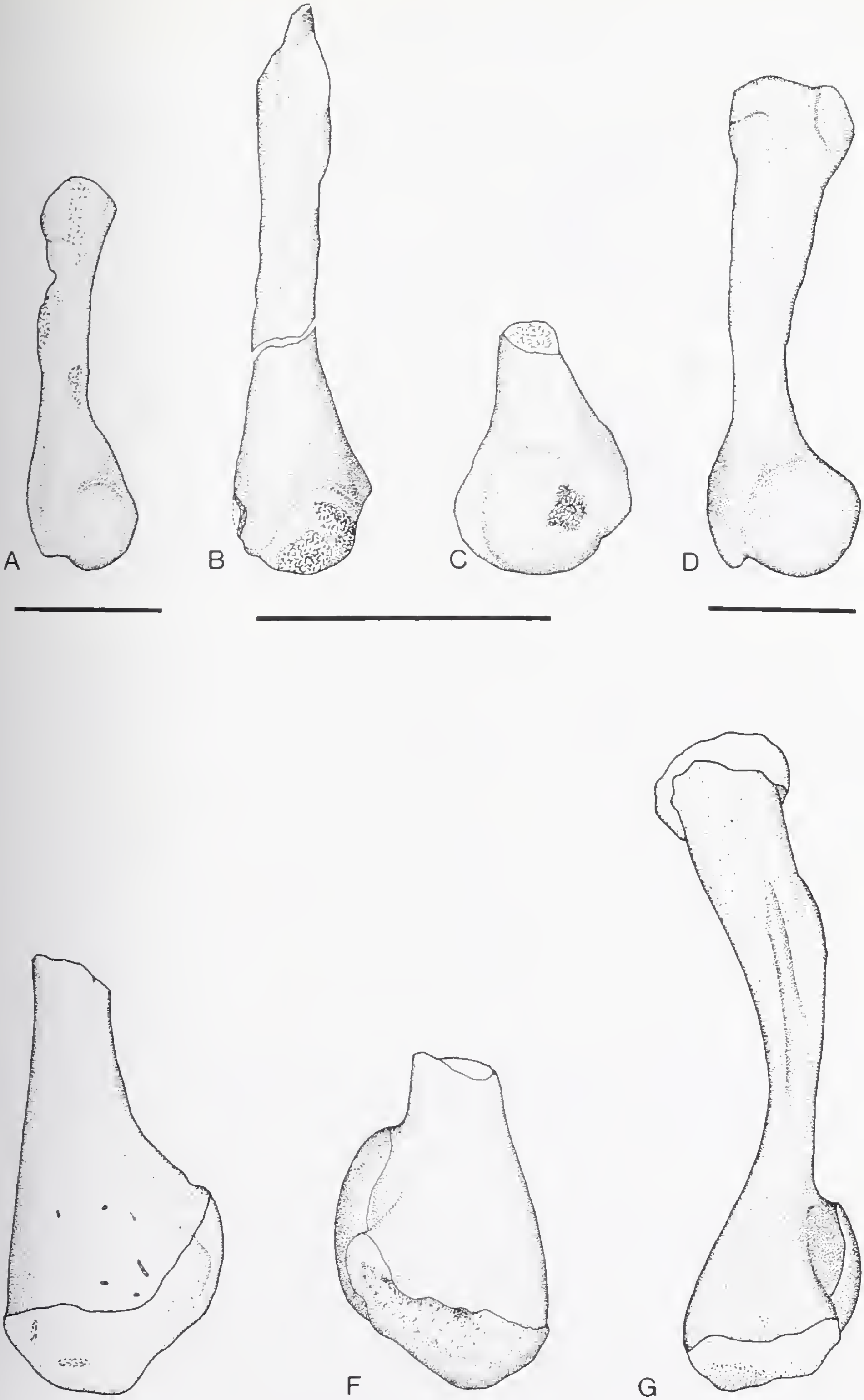
Fig. 22.—Comparison of humerus (A–D) and femur (E–G) in rhinophrynids. (A) *Eorhinophrynus* sp., YPM-PU 14664, left in ventral view; (B) *C. bayi,* CM 46763, left in ventral view; (C) *R. canadensis,* SMNH 1903, right in ventral view; (D) *R. dorsalis,* UMMZ 152331, left in ventral view; (E) *C. bayi,* CM 46761, distal end of right in medial view; (F) *R. canadensis,* SMNH 1920, distal end of left in medial view; (G) *R. dorsalis,* KU 84883, right in medial view. Scale bars = 5 mm.


A
B
C
D
E
F
G

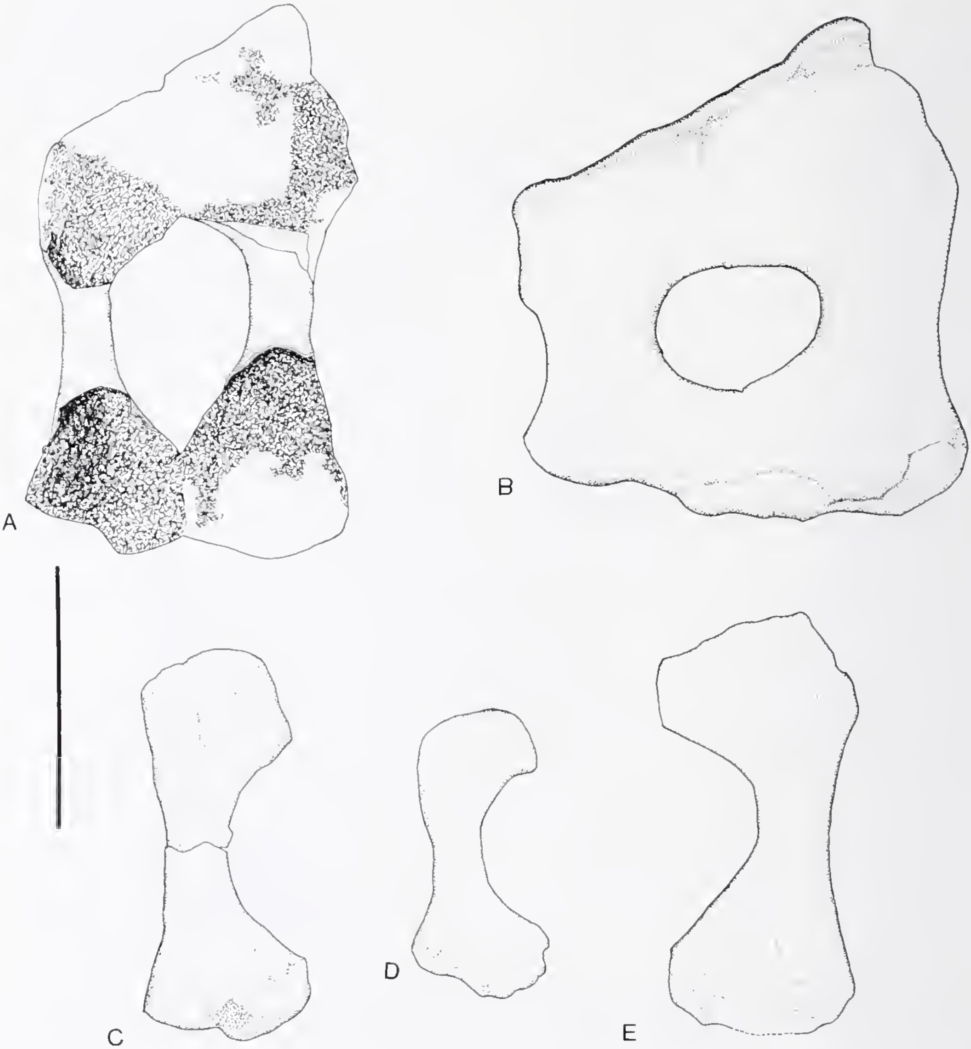


Fig. 23.—Comparison of tibiale and fibulare in rhinophrynids. (A) *C. bayi,* CM 46755, left in dorsal view; (B) *R. dorsalis,* KU 84885, left in dorsal view; (C) *Eorhinophrynus* sp., YPM-PU 21773, left tibiale in dorsal view; (D) *R. canadensis,* SMNH 1911, left tibiale in dorsal view; (E) *E. septentrionalis,* UCMP 113252, left fibulare in dorsal view. Scale bar = 5 mm.

in the outgroups, *C. bayi* and *R. dorsalis.* It is laterally broad with a square posterior margin in *E. septentrionalis* (Fig. 21A–C). The posteriorly tapering condition is judged the primitive state, and a broad, squared neural arch the derived state.

17. *Humeral ball.*—The humeral ball is oval in *Eorhinophrynus* sp. (Fig. 22A–D). It is round in the outgroups, *E. septentrionalis, C. bayi, R. canadensis,* and *R. dorsalis.* Therefore, a round humeral ball is considered the primitive condition and an oval humeral ball the derived state.

Two points of comparison not listed in the above character analysis need to be discussed.

Size.—Holman (1963, 1972) noted that *R. canadensis* is generally smaller than *R. dorsalis.* The majority of *R. canadensis* elements examined are incomplete making length measurements impossible. However, some elements appear to be as large as those from small specimens of *R. dorsalis.* Measurements of *C. bayi* overlap with the small end of the size range of *R. dorsalis* (Table 2). Most *C. bayi* specimens measured are young adults, whereas those of *R. dorsalis* are believed to be mature adults, which most likely accounts for the somewhat smaller size of *C. bayi* elements. The same may be true for *R. canadensis,* femora of which show varying degrees of ossification, suggesting that more than one ontogenetic stage is present.

Forelimb-to-hindlimb ratio.—The only proportion comparison made between *C. bayi* and *R. dorsalis* was the forelimb-to-hindlimb ratio. *Chelomophrynus bayi* has slightly longer hind limbs in relation to the forelimbs than *R. dorsalis* (Table 2). Dobrowolska (1973) has demonstrated that body-part proportions can undergo many changes in different directions between the completion of metamorphosis and sexual maturity. The skeletons of *C. bayi* in which the forelimb-to-hindlimb ratio was measured are young adults, whereas those of *R. dorsalis* are believed to be sexually mature adults. It is possible that the values obtained for *C. bayi* do not reflect what the values would be in a mature adult of this taxon.

RELATIONSHIPS

There is no reason to question the inclusion of *Chelomophrynus* in the family Rhinophrynidae based on its current definition. Of the many osteological characters used to define the family (see Systematic Paleontology above), only two could not be determined in *C. bayi*—the number of tarsalia and the phalangeal formula. *Chelomophrynus bayi* exhibits the remaining diagnostic osteological features.

The evolutionary history of rhinophrynids has been based on the few known fossils in this family. Hecht (1959) postulated that *Eorhinophrynus septentrionalis* is more specialized than *Rhinophrynus dorsalis* based on the structure of the atlas. Holman (1968, 1972) found no evidence excluding *R. canadensis* from the ancestry of *R. dorsalis* and later (1972) speculated that *E. septentrionalis* may have given rise to *R. canadensis.* Estes (1975) noted that *E. septentrionalis* could be placed as a primitive species in the genus *Rhinophrynus* and could possibly be ancestral to *R. dorsalis.*

In order to better understand the interrelationships of rhinophrynids, a cladogram was constructed using PAUP (version 2.4). Only characters which could reveal the interrelationships of rhinophrynids were used (Table 4). *Eorhinophrynus* sp. and *E. septentrionalis* (and characters 16 and 17 which apply only to them) were not included because they are incompletely known. The cladogram is arranged so that more primitive species are placed to the left.

This cladogram (Fig. 24), which has a consistency index of 0.895, shows that *Rhinophrynus canadensis* and *R. dorsalis* are more closely related to each other than either is to *Chelomophrynus bayi.* Furthermore, based on the number of apomorphies possessed by each species, *Chelomophrynus* is more primitive than *Rhinophrynus,* and *R. canadensis* is more primitive than *R. dorsalis.*

Chelomophrynus bayi is unique in three features (characters 1, 2, and 4) which are a triangular shape of the alary process of the premaxilla, anterior notch of the maxilla, and an elongate posterior process of the vomer. Two characters show homoplasy. *Chelomophrynus bayi* is convergent with *Scaphiopus* in character 5,

Table 4.—*Distribution of primitive and derived characters among rhinophrynids. 0 = primitive, 1 = derived, 2 = more derived, 9 = missing.*

	Character numbers																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Discoglossus pictus	0	0	0	0	0	0	0	0	1	0	9	9	0	0	0	0	0
Pelobates cultripes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Scaphiopus couchi	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Scaphiopus bombifrons	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Eorhinophrynus sp.	9	9	9	9	9	9	9	9	9	9	0	9	9	9	0	0	1
Eorhinophrynus septentrionalis	9	9	9	9	9	9	9	9	9	9	0	9	9	9	0	1	0
Chelomophrynus bayi	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	0
Rhinophrynus canadensis	9	9	9	9	9	9	9	9	9	1	1	1	2	1	0	0	0
Rhinophrynus dorsalis	0	0	1	0	0	1	2	1	1	0	1	1	2	1	1	0	0

the derived state of which is a vomer having an elongate postchoanal ramus. A reversal occurs in character 9, orientation of the transverse processes of the posterior presacral vertebrae, in which the outgroups and *R. dorsalis* have the derived state, anteriorly-oriented transverse processes (state unknown in *R. canadensis*), and *C. bayi* has undergone a reversal to the primitive state, laterally-oriented transverse processes.

Four synapomorphies unite *R. canadensis* with *R. dorsalis* (characters 11–14):

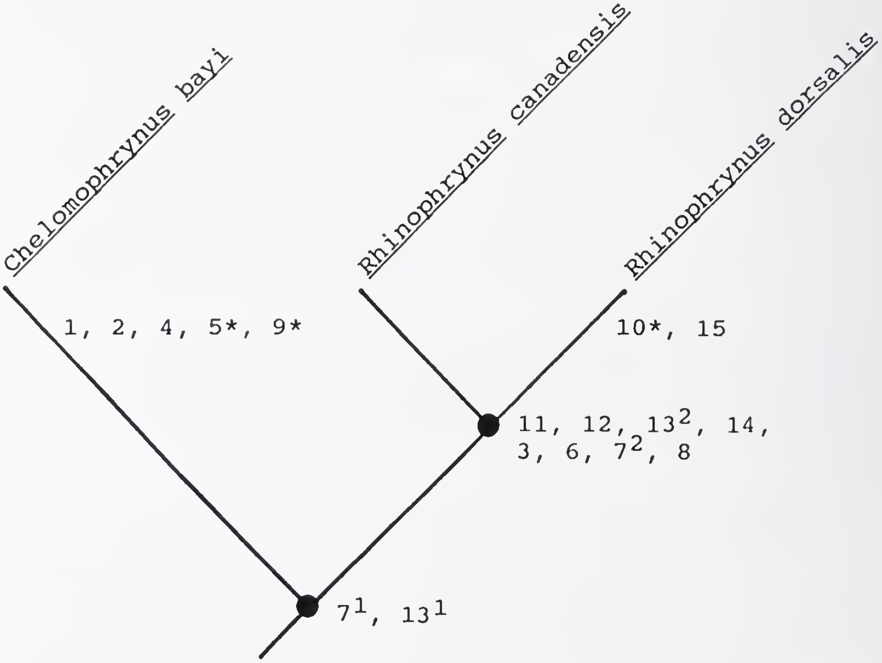


Fig. 24.—Cladogram illustrating hypothesized relationship of *Chelomophrynus bayi* to *Rhinophrynus canadensis* and *R. dorsalis*. Numbers refer to characters discussed in text. Asterisks are used to denote characters exhibiting homoplasy and numbers in superscript are used to indicate consecutively derived states. Characters 1–9 are unknown for *R. canadensis*.

a short, poorly-developed lateral crest of the humerus, a strongly-bowed femoral shaft, and a narrow shaft directly proximal to the distal condyles of the femur.

Four derived characters occur in *R. dorsalis* but not in *C. bayi*; their state is unknown in *R. canadensis.* These characters (3, 6, 7, and 8) are shown in the cladogram as synapomorphies between *R. canadensis* and *R. dorsalis,* although it is possible that some, or all, are autapomorphies for *R. dorsalis.* They are: the presence of a medial flange of the vomer, absence of a zygomatic ramus of the squamosal, a posteriorly-positioned orbitonasal foramen, and a fused cleithrum and suprascapula.

There are no known autapomorphies for *R. canadensis,* which is most likely a reflection of our incomplete knowledge of it. However, its combination of primitive and derived characters is unique for rhinophrynids.

Rhinophrynus dorsalis is unique in having a mediolaterally-oriented open area between the tibiale and fibulare. Character 10 exhibits homoplasy as *C. bayi* and *R. canadensis* have the derived state, a well-developed dorsal prominence, and *R. dorsalis* has the primitive state, a poorly-developed dorsal prominence. Either *C. bayi* and *R. canadensis* independently derived this character (convergence), or *R. dorsalis* underwent a reversal to the primitive state. The cladogram depicts this as a reversal for *R. dorsalis* although it is equally parsimonious for *C. bayi* and *R. canadensis* to have independently derived this character.

As mentioned, *Eorhinophrynus* sp. and *E. septentrionalis* were not included in the cladistic analysis because both are too incompletely known. Each species does possess an autapomorphy. *Eorhinophrynus* sp. has an oval humeral ball and *E. septentrionalis* has a laterally broad atlantal neural arch with a square posterior margin. Based on these autapomorphies, *Eorhinophrynus* sp. can be considered a distinct species, perhaps even a new genus as there are no synapomorphies uniting *Eorhinophrynus* sp. and *E. septentrionalis* in a single genus. However, it seems prudent to wait until these two species are better known before taxonomic changes are proposed.

ECOLOGY

Rhinophrynus dorsalis is highly adapted for burrowing, using its hind legs alternately or together to dig a burrow that is occupied for one day to as long as a month (Foster and McDiarmid, 1983). It is able to burrow directly after the completion of metamorphosis, when it leaves the pond for a terrestrial, fossorial existence (Foster and McDiarmid, 1983). Trueb and Gans (1983) theorized that it may burrow to feed on ants and termites, in addition to avoiding desiccation. They further theorized that *R. dorsalis,* upon reaching an ant or termite tunnel, forcibly scraped with its snout to form an opening through which it could catch the insects with its sticky, protrusible tongue. The burrowing mode of life is reflected in the skeleton of *R. dorsalis* by robust limb bones and two digging spades on each hind limb.

Specializations for burrowing have been observed in fossil rhinophrynids by previous workers. The atlantal neural arch of *Eorhinophrynus septentrionalis* is extremely long and broad, and Hecht (1959) suggested that it may have restricted movement in the neck region, allowing the head to be used as a ramrod while burrowing. In both *E. septentrionalis* and *Eorhinophrynus* sp., the proximal tarsals are robust, although not as robust as in *R. dorsalis,* which led Estes (1975) to speculate that both species of *Eorhinophrynus* were burrowers, but less efficient ones than *R. dorsalis.* Holman (1963, 1968, 1972) noted that *R. canadensis* has less robust limb bones than *R. dorsalis,* suggesting that it is a less efficient burrower than *R. dorsalis.*

The fossils of *Chelomophrynus bayi* are preserved in the shore line facies of a lake deposit (Bay, 1969). Evidence for transport of the specimens into this environment is lacking. The bones, many of which are thin and fragile, show no abrasion and many of the skeletons are articulated, or the elements closely associated. That *C. bayi* is a burrowing anuran is indicated by its robust limb bones and two digging spades on each hind limb. In contrast to *R. dorsalis, C. bayi* does not seem to have left the lake directly after metamorphosis as demonstrated by the overwhelming number of subadults (Stage V) collected from this deposit (Fig. 25). Furthermore, specimens at Stage V far outnumber those at stages I–IV and VI (Fig. 25). A possible reason for the greater number of Stage V individuals is because their larger and better ossified bones were more apt to have been preserved than the bones of younger stages.

Bones of Stage VI individuals would have been as readily preserved as those of Stage V animals so other reasons are needed to explain their low numbers. Age-specific mortality is a possible explanation. Many anurans, including *R. dorsalis,* produce large numbers of eggs few of which survive to maturity. For example, Zug and Zug (1987) estimated for *Bufo marinus* a 0.5% survival rate from egg to adulthood. Furthermore, they postulated that the highest mortality rate would occur during and directly after metamorphosis. Therefore, for *C. bayi* it is probable that there were fewer adults (Stage VI?) than subadults, as the subadults had a higher mortality rate. It is also probable that upon reaching Stage VI, the anurans left the lake for a terrestrial, burrowing existence. This could further account for the low number of Stage VI specimens preserved in the lacustrine deposit.

Rhinophrynus dorsalis may be a relict of what once was a widespread and slightly more diverse group of rhinophrynids which inhabited western interior basins during the Paleogene. Holman (1968) hypothesized that deterioration of the climate during the middle to late Tertiary caused the rhinophrynids to withdraw from the north. The late Paleocene climate in this region was warm-temperate, with abundant precipitation and no dry season (Hickey, 1977). A warming trend continued from the late Paleocene to early Eocene when a subtropical, equable climate predominated (Hickey, 1977). By the middle Eocene in Wyoming, the climate became dryer and more tropical, with rainy and dry seasons (Macginitie, 1969, 1974). The late Oligocene climate at Cypress Hills, where *R. canadensis* lived, is thought to have been dry with seasonal rainfall (Holman, 1968). The climate continued to become less equable, drier, and cooler throughout the Tertiary (MacGinitie, 1974), and deteriorated much more during the Pleistocene. Rhinophrynids appear to have adapted to drier conditions by becoming increasingly specialized for burrowing, which would enable them to avoid desiccation. Therefore, it seems doubtful that drier conditions with less rainfall caused them to leave the north. Most likely, it was the decrease in temperature that caused rhinophrynids to withdraw from the north to their present range in coastal lowlands in extreme southern Texas, Mexico, and Central America. The fact that *R. dorsalis* currently inhabits seasonally dry, tropical forests further supports this theory.

CONCLUSIONS

The Eocene beds at Battle Mountain range from late Bridgerian to Uintan in age.

Chelomophrynus bayi is distinct from other rhinophrynids in having a triangular

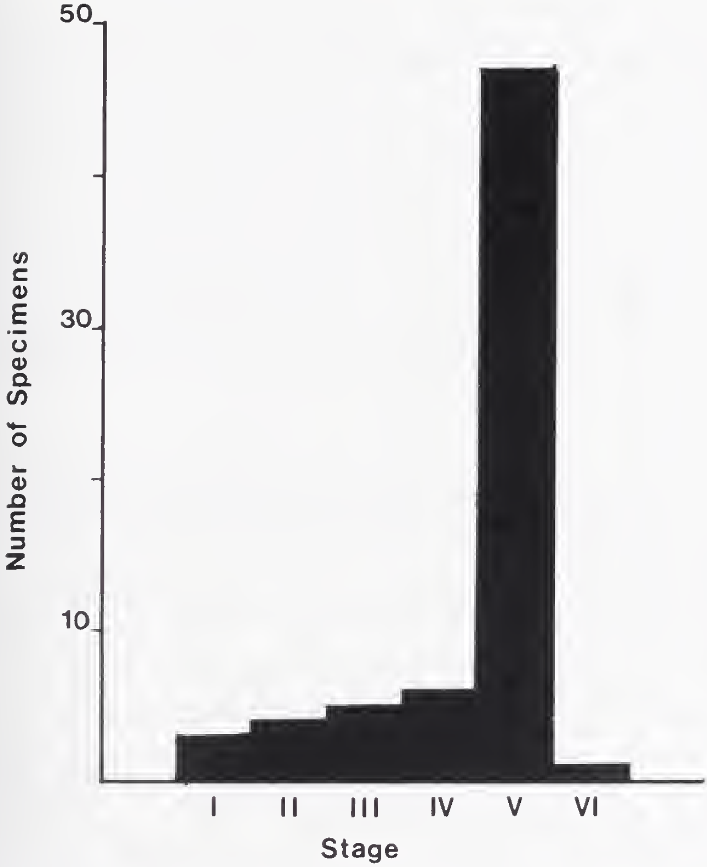


Fig. 25.—Histogram showing number of specimens in each growth stage.

alary process of the premaxilla, an anterior notch of the maxilla, an elongate posterior process of the vomer, an elongate postchoanal ramus of the vomer, and laterally-oriented transverse processes of the last three presacral vertebrae.

Chelomophrynus is more primitive than *Rhinophrynus.* The relationship of *Eorhinophrynus* to *Chelomophrynus* and *Rhinophrynus* cannot be determined at this time.

The presence of two digging spades on each hind limb and the somewhat robust skeleton of *C. bayi* suggest that it was a burrowing anuran.

Tadpoles and subadults of *C. bayi* inhabited the Eocene lake, but it seems likely that adults lived in the terrestrial environment.

Rhinophrynids may have been a widespread group during the Paleogene. Cooling temperature during the middle to late Tertiary most likely caused them to leave southern Canada and the western interior of the United States to their present range in the coastal lowlands of extreme southern Texas, Mexico, and Central America.

ACKNOWLEDGEMENTS

This publication is, in part, a revision of a master's thesis submitted to the University of Pittsburgh. I am indebted to my committee members for their support and guidance throughout the course of this research: M. R. Dawson, J. Donahue, and L. Krishtalka. I also thank the following people for their helpful advice and correspondence: A. Holman, C. A. M. Meszoely, Z. V. Špinar, L. Trueb, and R. J. Wassersug. Special thanks are due to D. S Berman who patiently assisted me in ways too numerous to list. David C. Cannatella and two anonymous reviewers provided many helpful comments.

I am grateful to the following for the loan of specimens in their care: E. S. Gaffney, AMNH; J. H. Hutchison, UCMP; C. J. McCoy and E. J. Censky, CM; R. J. Wassersug, Dalhousie University; L. Trueb, KU; A. G. Kluge and R. A. Nussbaum, UMMZ; J. A. Holman, MSU; J. H. Ostrom, YPM-PU; and J. E. Storer, SMNH. The field work could not have been accomplished without the support and assistance of Drs. L. Krishtalka and R. K. Stucky, and field assistants Patrick V. McShea and Ellen A. Henrici. Mr. Allen Campbell helped run the PAUP program, and Ms. Elizabeth Hill and Ms. Mary Ann Schmidt provided assistance on the computer.

A Sigma-Xi grant-in-aid of research provided funds for travel to Northeastern University, Boston, Massachusetts. Funding for the field work came from the following grants awarded to Drs. Krishtalka and Stucky: National Science Foundation Grants BSR-8709242 and BSR-8402051, NASA Grant NAGW-949, and the Netting Research Fund. Ms. Ellen A. Henrici generously provided a field vehicle for the 1986 field season.

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ANNALS OF CARNEGIE MUSEUM
VOL. 60, NUMBER 2, PP. 145–162 23 MAY 1991

NEW TEIID LIZARDS FROM THE UPPER CRETACEOUS OLDMAN FORMATION (JUDITHIAN) OF SOUTHEASTERN ALBERTA, CANADA, WITH A REVIEW OF THE CRETACEOUS RECORD OF TEIIDS

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ABSTRACT

Four new genera and five new species of Teiidae (Lacertilia), based on newly discovered specimens from the Upper Cretaceous Oldman Formation (Judithian), Alberta, Canada, are named and described. A brief review of the Cretaceous record of the Teiidae in both North America and central Asia is presented. Recognition of the new teiids and work in progress shows that, contrary to previous authors, the North American Judithian lizard fauna is significantly different taxonomically from that of Lancian age and, hence, represents a previously unrecognized episode in the evolutionary history of teiids. The stratigraphic distribution of teiid fossils in the Cretaceous of North America suggests that the unicuspid tooth form is primitive for the family Teiidae.

INTRODUCTION

Although the Oldman Formation (Russell and Landes, 1940) of Alberta has yielded a large vertebrate fauna, lizards are poorly known compared to dinosaurs and other vertebrates from the formation. The earliest report concerning terrestrial lizards from the Oldman Formation was in 1923, when Gilmore referred a dorsal vertebra (UA 112) to a "lacertian" (=lacertilian). The specimen was collected by G. F. Sternberg in 1921 from Sandy Point, South Saskatchewan River, north of Medicine Hat. Subsequently, Gilmore (1928) referred this specimen to *Palaeosaniwa canadensis,* a large varanid, and Russell (1964) and Langston (1965) included *Palaeosaniwa canadensis* in their lists of Oldman vertebrate species. The first report on teiids from the Oldman Formation was by Waldman (1970), who described a lower jaw (NMC 13563) from a locality near Steveville, southeastern Alberta, referring it to *Chamops* sp. (see later discussion on the specimen in this paper). Other records of teiids are included in faunal lists given by Fox (1976), Currie (1986), Eberth (1987), and Koster et al. (1987). The Judithian age of the Oldman Formation was established by Russell (1964, 1975; and see Lillegraven and McKenna, 1986). The Judithian Land Mammal Age is approximately equivalent to mid-Campanian time (Russell, 1975; Eberth, 1987); beds containing Judithian vertebrates in Alberta and Montana have yielded radiometric ages from 74 to 78 my (Eberth, 1987; Goodwin and Deino, 1989; Thomas et al., 1990).

This paper describes several new teiids from the Oldman Formation, Alberta,

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Submitted 1 May 1990.

and presents a brief review of the Cretaceous record of the family. Four new genera and five new species are named herein, based on specimens collected from the Irvine and Railway Grade localities, southeastern Alberta (legal descriptions below). Recognition of these new taxa and work in progress on others shows that, contrary to previous authors (Sahni, 1972; Armstrong-Ziegler, 1980; Sullivan, 1981; Estes, 1983*a*), the North American Judithian lizard fauna is significantly different taxonomically from that of Lancian age (see Estes, 1964, 1983*a*; Estes et al., 1969), resembling in that respect the mammalian fauna, which has fewer than 10% of the species in common between Judithian and Lancian horizons (see Lillegraven and McKenna, 1986). Detailed description and more extensive discussion of the taxa named here will be published elsewhere as part of a monographic treatment of lizards from the Upper Cretaceous of western Canada being undertaken by the first author.

Terminology used in the text follows Estes (1964, 1983*a*), but with some terms explicitly defined as follows: inferior alveolar foramina—a row of mental foramina located along the lateral surface of the dentary; subdental shelf—a shelf-like medial extension of the dentary below the tooth row (often contributing to the splenodentary articulation); subpleurodont—attachment of the marginal teeth to the medial surface of the lateral parapet, which remains low (one half or less of crown height, a condition commonly seen in teiids); sulcus dentalis—also called "dental gutter", a groove developed medial to the tooth bases, separating the tooth row from the subdental shelf.

Institutional abbreviations are as follows: UALVP (=UA), Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology, University of Alberta, Edmonton, Alberta, Canada; NMC, National Museum of Natural Science, Ottawa, Ontario, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.; UNM, University of New Mexico, Albuquerque, New Mexico, U.S.A.; SMU, Southern Methodist University, Dallas, Texas, U.S.A.; YUM (=YPM), Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

SYSTEMATIC PALEONTOLOGY

Class Reptilia Linnaeus, 1758
Subclass Diapsida Osborn, 1903
Infraclass Lepidosauromorpha Benton, 1983
Superorder Lepidosauria Haeckel, 1866
Order Squamata Oppel, 1811
Suborder Lacertilia Owen, 1842
Infraorder Scincomorpha Camp, 1923
Family Teiidae Gray, 1827 (*sensu* Estes, 1983*a*; Presch, 1983)

Boulenger (1885) subdivided the family Teiidae (*sensu lato*) into four groups. Lizards in "group I" were later informally designated as "macroteiids", and those in "groups II–IV", "microteiids" (Ruibal, 1952; MacLean, 1974). MacLean (1974) and Presch (1974*a*) recognized macroteiids and microteiids as separate subfamilies (Teiinae and Gymnophthalminae). More recently, Estes (1983*a*) and Presch (1983) independently ranked the two groups as families.

Teiidae (*sensu stricto*) in this paper refers to Boulenger's group I, and is used in the sense of Estes' (1983*a*) and Presch's (1983) definition. In the most recent study of the phylogenetic relationships of the lizard families, Estes et al. (1988)

recognized 14 synapomorphies for the family Teiidae, among which the following are unambiguous and reliable character states for fossil teiid studies: replacement teeth developing in deep subcircular cavities at tooth bases (Romer, 1956); cementum deposited extensively on tooth bases (Presch, 1974*b*); vomers elongate, approaching pterygoids (Romer, 1956); splenial large, extending anteriorly to the symphysis, leaving only a small symphysial foramen (MacLean, 1974). We note as well that teiids often exhibit a well-developed sulcus dentalis and subdental shelf (Estes et al., 1988), character states that are often useful in determining the affinities of species that are represented by the incomplete jaws that make up most of the North American record of identifiable Cretaceous lizards.

For the higher classification of lizards we follow Carroll (1988*a*) in the belief that an important attribute of classifications is retention of relative stability to permit ease of communication (see Martin, 1990:99), even in the face of changing views of cladistic relationships (compare, e.g., Benton, 1985; Carroll, 1988*b*; Gauthier et al., 1988; Estes et al., 1988).

Glyptogenys, new genus

Type species.—*Glyptogenys ornata,* new species.

Diagnosis.—As for the type and only known species.

Etymology.—*glyptos* + *genys* (Gr.), meaning "carved jaw", in reference to the ornamented dentary of this lizard.

Glyptogenys ornata, new species
(Fig. 1)

Holotype.—UALVP 29735, anterior part of a left dentary bearing 12 well-preserved teeth, only known specimen.

Type locality and horizon.—Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta.

Age.—Late Cretaceous (Judithian).

Diagnosis.—A teiid lizard that differs from other fossil and Recent teiids in having the following combination of characters: dentary deep, massively built, and heavily ornamented below inferior alveolar foramina in at least adult individuals; subdental shelf deep and robust; teeth subpleurodont, with lateral parapet about half of crown height; crowns mostly bicuspid with main cusp in posterior position on crown and anterior cusp low and rounded; anterior teeth unicuspid and more nearly conical; tooth bases compressed anteroposteriorly, with thick, ring-like basal deposit of cementum.

Etymology.—*ornata* (L.), meaning "ornamented", in reference to the sculpture on the external surface of the holotype.

Remarks.—Although several uncatalogued specimens in the UALVP collections show a jaw configuration that resembles that of the holotype, they are too fragmentary to be referred to *Glyptogenys ornata* with complete certainty, leaving UALVP 29735 to be the type and only known specimen for this new lizard at present.

The assignment of *Glyptogenys ornata* to the family Teiidae is mainly founded on the conspicuous basal deposit of cementum around the tooth bases, and the presence of a hypertrophied splenial that extends well anteriorly as indicated by the widely open Meckelian sulcus in the holotype. These are diagnostic characters of the Teiidae (MacLean, 1974; Presch, 1974*b*; Estes, 1983*a*; Estes et al., 1988). Other characters shown by the holotype and often occurring in teiids, such as the

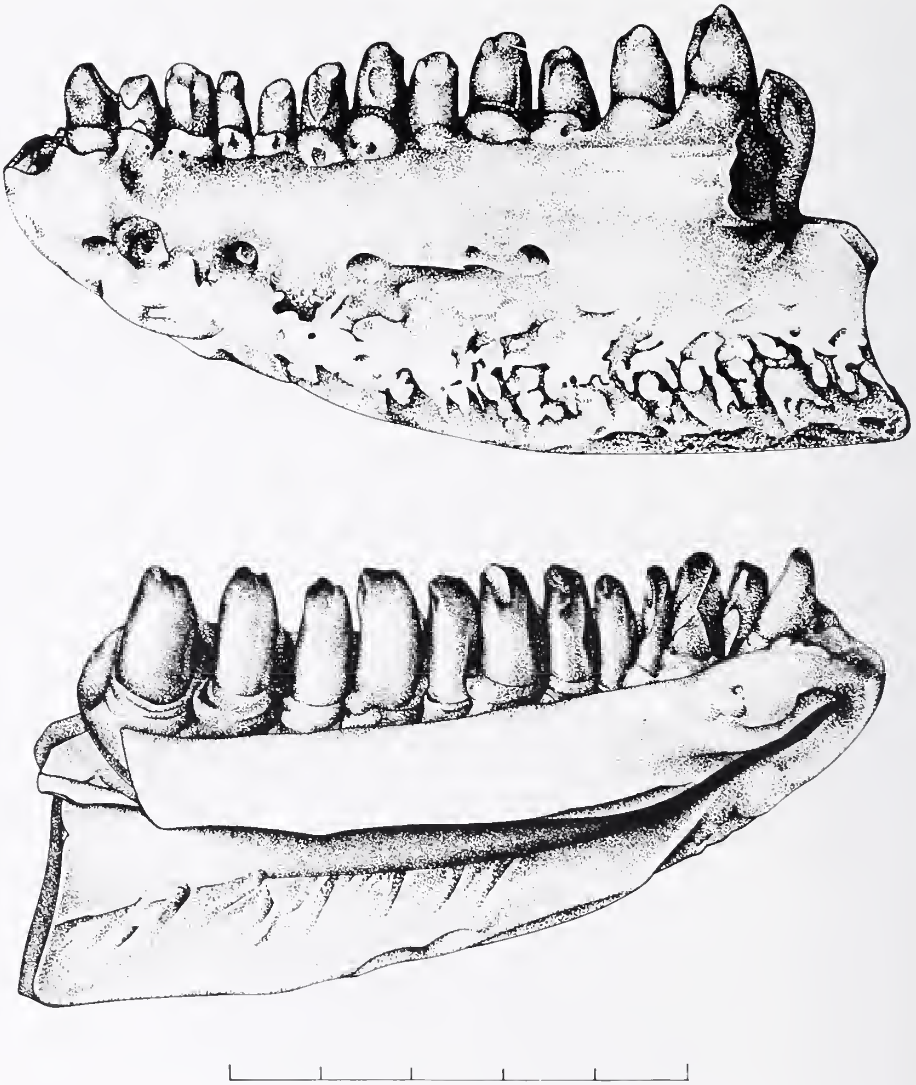

Fig. 1.—*Glyptogenys ornata* new genus and species, Oldman Formation (Judithian), Upper Cretaceous; UALVP 29735 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

subpleurodont dentition, enlarged bicuspid teeth, well-developed subdental shelf, and sulcus dentalis (see, e.g., Estes, 1964; Winkler et al., 1990), reinforce our conclusion that *G. ornata* is a teiid. *G. ornata* can be readily distinguished from Lancian *Chamops segnis* Marsh 1892, which is similar in size, by its bicuspid, closely-spaced, and somewhat recurved dentary teeth that lack swollen, barrel-like shafts; further, the dentary of *G. ornata* is deeper anteriorly, while that of *Chamops* lacks sculpture (Estes, 1964).

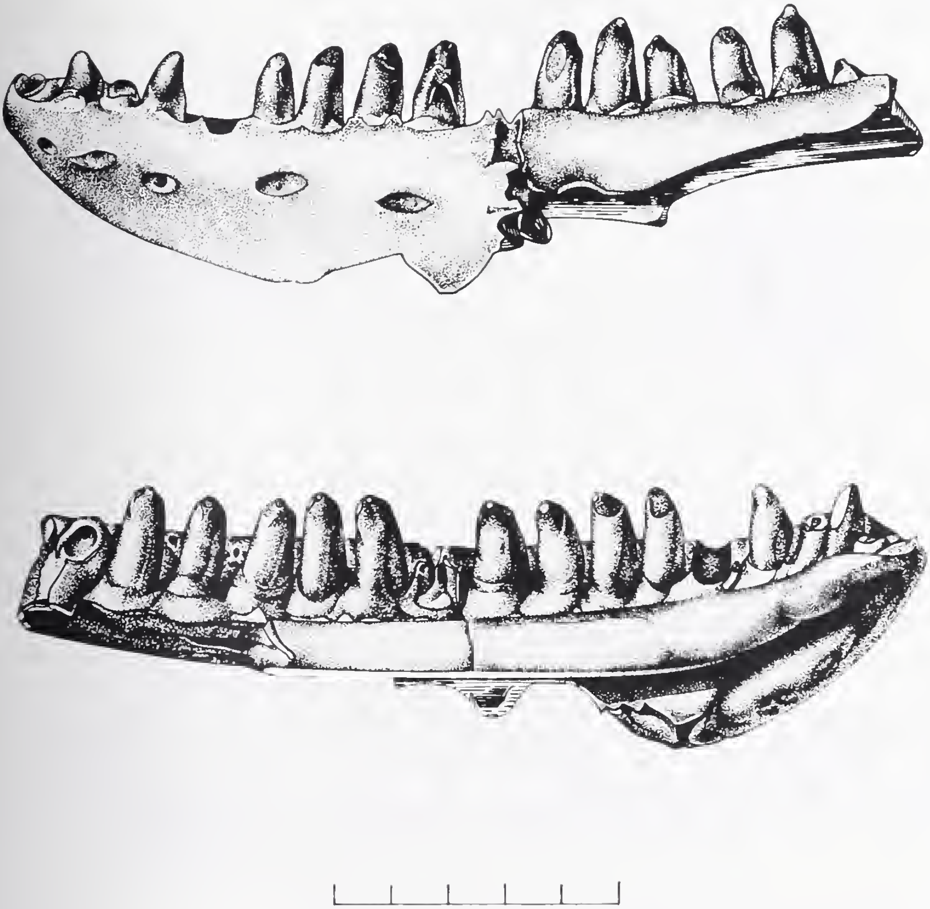

Fig. 2.—*Socognathus unicuspis* new genus and species, Oldman Formation (Judithian), Upper Cretaceous; UALVP 29739 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

Socognathus, new genus

Type species.—Socognathus unicuspis, new species.

Diagnosis.—As for the type and only known species.

Etymology.—sokos + gnathos (G.), meaning "strong jaw".

Socognathus unicuspis, new species
(Fig. 2)

Holotype.—UALVP 29739, an incomplete left dentary bearing 11 well-preserved teeth and bases of six others.

Type locality and horizon.—Railway Grade, Dinosaur Provincial Park, in S 22, Tp. 20, R 12, W 4, southeastern Alberta; Oldman Formation.

Age.—Late Cretaceous (Judithian).

Referred specimens.—UALVP 29736, 29740, 29743–45 (total: 5); all are incomplete dentaries bearing teeth and broken tooth bases, and all were collected from the Irvine locality.

Diagnosis.—Relatively large teiid differing from other teiids in having the unique combination of the following characters: dentary long and robust; mandibular symphysis strongly enhanced by ventral bony buttress; teeth unicuspid, slightly compressed anteroposteriorly, and mostly large, but variable in spacing and recurvature of crowns; tooth attachment subpleurodont, with lateral parapet low, about one-third of crown height; crowns with moderately strong anterior ridge and weaker posterior ridge curving ventrolingually from apical cusp.

Etymology.—*unicuspis* (L.), in reference to the single-cusped dentary teeth of this lizard.

Remarks.—*Socognathus unicuspis* is founded on six relatively well-preserved specimens, four left and two right dentaries; several uncatalogued, more fragmentary dentaries are also in the collection from both Railway Grade and Irvine localities. Together, the type and referred specimens allow reconstruction of the proportions of the dentary of *S. unicuspis* posteriorly to the most posterior tooth position. These proportions differ significantly from those of the dentary of *Glyptogenys ornata,* the other relatively large teiid from the Oldman Formation, Alberta; the lack of sculpture and the irregularly developed dentition also contrast with *Glyptogenys.* The combination of large, irregularly spaced, nearly conical, unicuspid teeth and the strong mandibular symphysis enhanced by the bony buttress is unique among known teiids of Late Cretaceous age; the buttress is more prominent in larger specimens of *S. unicuspis* and contrasts with the absence of a comparable structure in the dentaries of *Glyptogenys* and *Leptochamops,* for example, among Cretaceous teiids. The large size of this lizard and the tendency of the teeth to increase in size posteriorly (resulting in a certain degree of heterodonty), may suggest relationship with the subfamily Tupinambinae, which includes the Recent genera *Tupinambis, Callopistes, Crocodilurus, Dracaena,* and fossil *Chamops* (Presch, 1983).

Sphenosiagon, new genus

Type species.—*Sphenosiagon simplex,* new species.

Diagnosis.—As for the type and only known species.

Etymology.—*sphen* + *siagon* (Gr.), meaning "wedge jaw", in reference to the shape of the lower jaw of this lizard.

Sphenosiagon simplex, new species
(Fig. 3)

Chamops sp. Waldman, 1970:546, fig. 2–3.

Holotype.—UALVP 29742, a fragmentary left mandible having splenial firmly articulated with the dentary, and having eight posterior teeth and the base of the last dentary tooth.

Type locality and horizon.—Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta.

Age.—Late Cretaceous (Judithian).

Referred specimen.—NMC 13563, a right mandibular ramus from the Oldman Formation near Steveville, southeastern Alberta (Waldman, 1970).

Diagnosis.—Differing from other known teiids, including Lancian *Chamops segnis,* in having the unique combination of the following characters: dentary

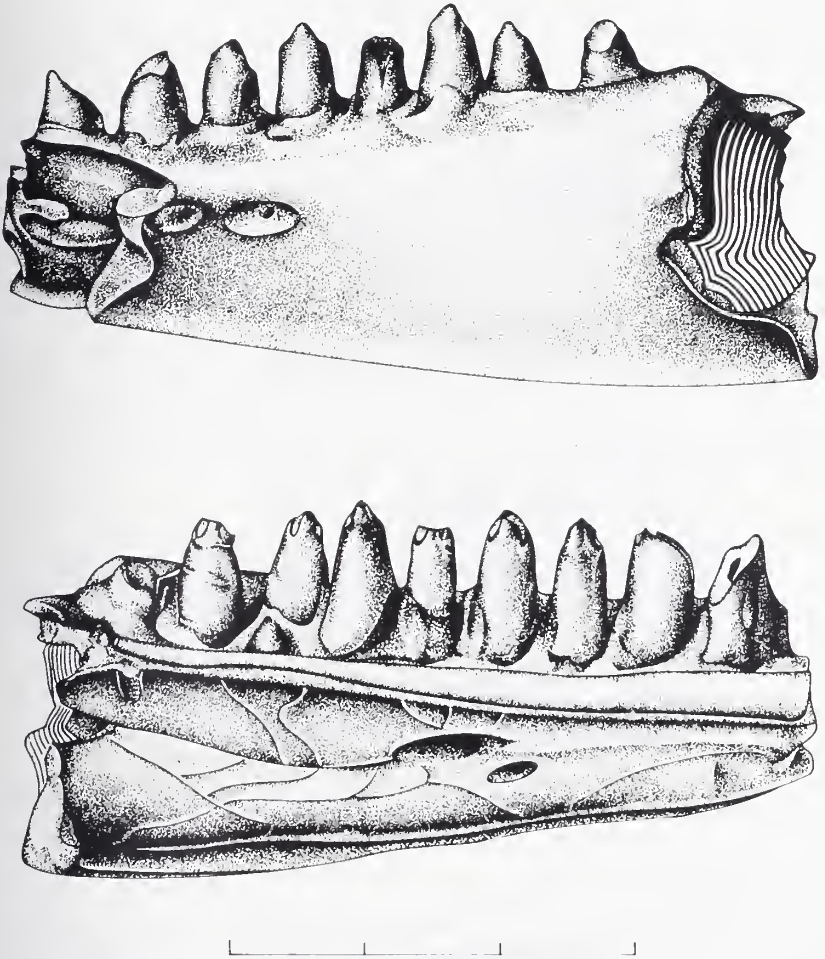

Fig. 3.—*Sphenosiagon simplex* new genus and species, Oldman Formation (Judithian), Upper Cretaceous; UALVP 29742 (holotype), incomplete left mandible; (above) lateral view, (below) medial view. Scale = 3 mm.

slender, lightly built, and wedge-shaped; subdental shelf narrow; sulcus dentalis poorly defined; teeth unicuspid; tooth attachment subpleurodont, with lateral parapet about half of crown height.

Etymology.—*simplex* (L.), in reference to the simple tooth form of this lizard.

Remarks.—The referral of UALVP 29742 to the family Teiidae is indicated by several characters shown on the specimen, including a large splenial and the extensive basal deposit of cementum around the tooth bases.

In 1970, Waldman described an incomplete right mandible of a lizard (NMC 13563) from the Oldman Formation, near Steveville, Alberta. The specimen was originally identified as *Chamops* sp. (Waldman, 1970), but was subsequently referred to the Lancian species, *Chamops segnis* (Estes, 1983*a*). Our restudy of the specimen indicates that it is best referred to *Sphenosiagon,* not to *Chamops.*

A comparison of NMC 13563 with the holotype of *S. simplex* shows that the two specimens are closely similar: they show the same unique jaw shape, the same development of the splenial, a slender subdental shelf, poorly defined sulcus dentalis, and the same type of tooth attachment; clearly, NMC 13563 belongs to *S. simplex.* The tooth crowns on NMC 13563 have been partially dissolved diagenetically; however, those on UALVP 29742 are unambiguously unicuspid, not tricuspid, as in *C. segnis,* nor do the crowns display the barrel-like proportions that Estes (1983*a*: fig. 22) illustrated for NMC 13563; in fact, Estes' (1983*a*) figure of NMC 13563 differs substantially from that of Waldman (1970: fig. 2), which is the more accurate, and has been drawn so that it appears to be more *Chamops*-like than it is. For example, no "surangular window" is preserved on NMC 13563 (see Estes, 1983*a*), and the "coronoid", which both Waldman (1970) and Estes (1983*a*) have shown, is actually a broken part of the jaw glued into the position of a coronoid (Gao, in progress). Hence, Estes' (1983*a*) conclusion that *Chamops* is a member of the Tupinambini must come from evidence other than that provided by this specimen, which does not pertain to *Chamops.*

Gerontoseps, new genus

Type species.—Gerontoseps irvinensis, new species.

Diagnosis.—As for the type and only known species.

Etymology.—gerontos + *seps* (Gr.), meaning "old man lizard" (lizard from the Oldman Formation).

Gerontoseps irvinensis, new species

(Fig. 4)

Holotype and only known specimen.—UALVP 29754, an anterior part of a right mandible having three complete and ten broken teeth.

Type locality and horizon.—Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta; Oldman Formation.

Age.—Late Cretaceous (Judithian).

Diagnosis.—A small species differing from other Late Cretaceous and Recent teiids in having the following combination of characters: dentary shallow but wide, convex both laterally and medially; splenial fused to dentary; sulcus dentalis narrow and conspicuously deep; teeth unicuspid and nearly conical, but having symmetrical anterior and posterior ridges; tooth attachment subpleurodont, with lateral parapet about one-third of crown height.

Etymology.—Irvine, place name, in reference to the village near the type locality.

Remarks.—One of the most obvious characters of the holotype is the co-ossification between the well-developed splenial and the dentary along the dorsal splenodentary suture; splenodentary fusion is characteristic of xantusiid lizards and is also seen in the Lancian teiid *Haptosphenus* (Estes, 1964), both of which are very different from UALVP 29754 in other aspects of jaw construction and dentition. We interpret this fusion as taxonomically significant, owing to the small size of UALVP 29754 and the low probability that such extensive fusion would occur in a still young individual of a species in which adult size was significantly larger than is indicated by the dimensions of UALVP 29754. The deep sulcus dentalis and unicuspid crowns are other features that allow UALVP 29754 to be readily distinguished from the dentaries of other Late Cretaceous teiids. The deep sulcus, well-developed subdental shelf and splenial, and prominent subcircular

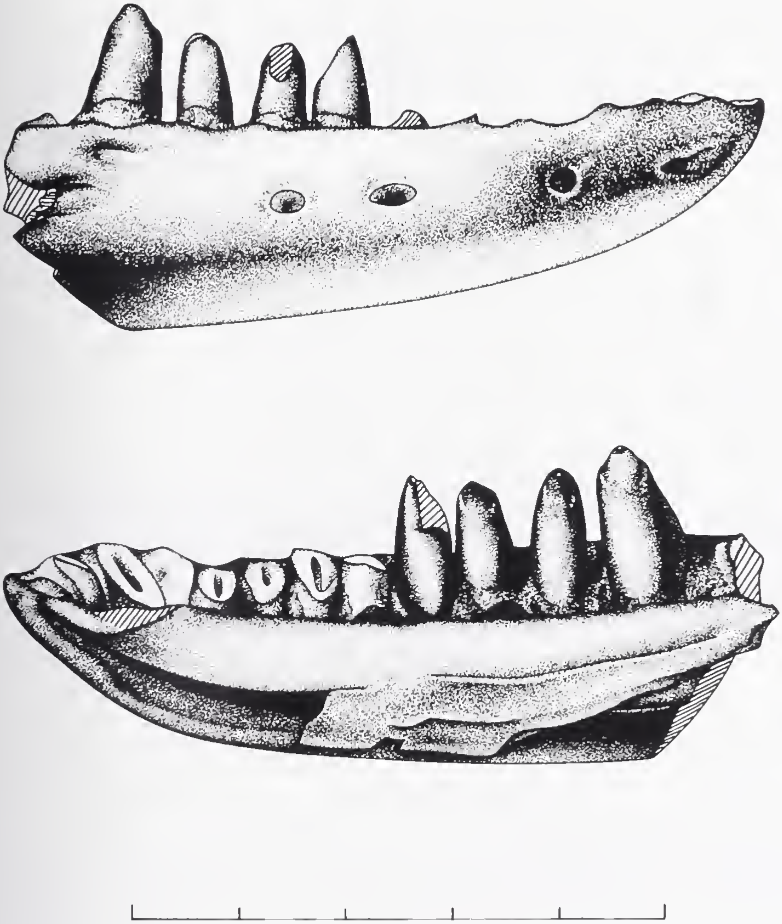

Fig. 4.—*Gerontoseps irvinensis* new genus and species, Oldman Formation (Judithian), Upper Cretaceous; UALVP 29754 (holotype), incomplete right mandible; (above) lateral view, (below) medial view. Scale = 5 mm.

basal replacement pits (at five tooth positions on UALVP 29754) are all consistent with classification of *Gerontoseps* in the Teiidae.

Leptochamops Estes, 1964
Leptochamops thrinax, new species
(Fig. 5)

Holotype.—UALVP 29749, an incomplete left dentary bearing five teeth and bases for ten others.

Referred specimens.—UALVP 29748, 29750, 29753; all are incomplete dentaries having several teeth preserved and collected from the Irvine locality.

Type locality and horizon.—Outcrop of the Oldman Formation near Irvine, in S 31, Tp. 11, R 2, W 4, about 40 km east of Medicine Hat, southeastern Alberta.

Age.—Late Cretaceous (Judithian).

Diagnosis.—A species of *Leptochamops* differing from the Lancian *L. denticula-*

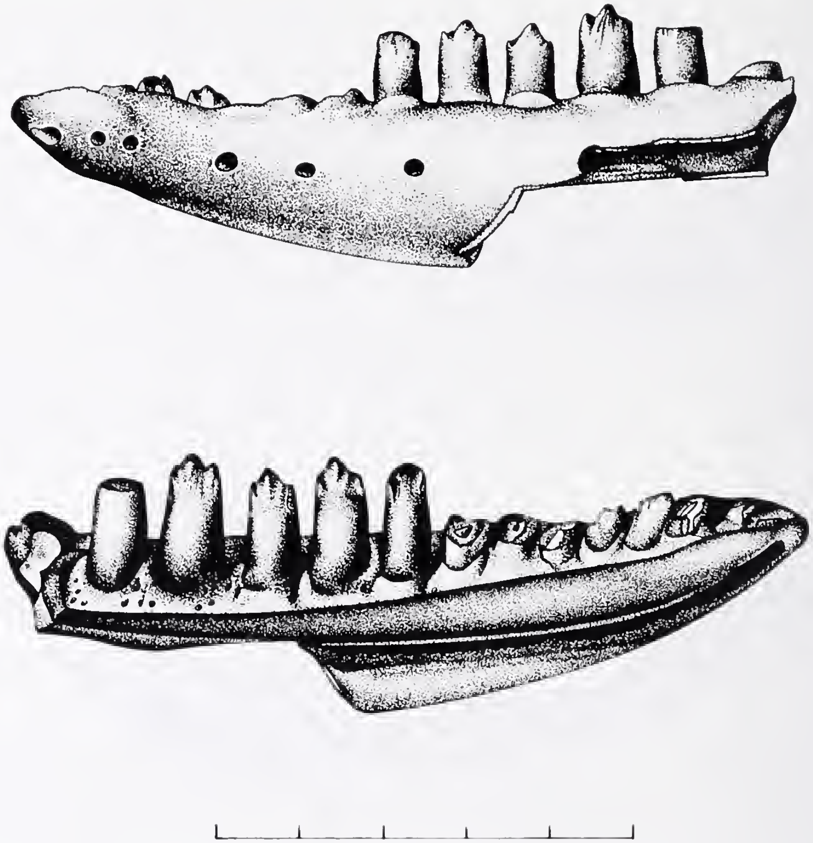

Fig. 5.—*Leptochamops thrinax* new species, Oldman Formation (Judithian), Upper Cretaceous; UALVP 29749 (holotype), incomplete left dentary; (above) lateral view, (below) medial view. Scale = 5 mm.

tus in having strongly tricuspid, widely spaced, and fewer dentary teeth; and having a nearly straight tooth row, lacking the characteristic curvature seen in the Lancian species; tooth attachment subpleurodont, with lateral parapet one-half to one-third of crown height and decreasing posteriorly.

Etymology.—*thrinax* (Gr.), in reference to the broadly tricuspid teeth of this species.

Remarks.—The holotype, UALVP 29749, shows characters, such as long, shallow symphysis, shallow dentary, shallow Meckelian sulcus, and high crowned, straight, and columnar tricuspid teeth, that indicate it is referrable to the genus *Leptochamops* Estes 1964, but these same features readily distinguish the type and referred dentaries of *L. thrinax* from those of the other teiids from the Oldman Formation described above, including *Gerontoseps,* which evidently was similar in size. When compared to *L. denticulatus,* a Lancian species, its strongly tricuspid, widely spaced dentary teeth (which are also fewer in number) and straight tooth row indicate that the specimen represents a new species of the genus. The inclusion of UALVP 29750 and 29753 in this species is based on their similar jaw configuration, tooth number, and straight tooth row; the tooth crowns on the latter two specimens are partly dissolved away. Another specimen, UALVP 29748, shows the same distinctive cusp pattern and jaw configuration as the holotype, but has tooth bases that are more swollen, and is larger; these differences appear best interpreted as ontogenetic, and we include UALVP 29748 in *L. thrinax* accordingly.

REVIEW OF THE CRETACEOUS RECORD OF TEIIDS

The family Teiidae (*sensu* Estes, 1983*a*; Presch, 1983) includes about 20 genera, half of which are extinct (Presch, 1983). This paper adds four new genera and five new species; four of these species exhibit a lower dentition in which the crowns are unicuspid or weakly bicuspid, which may be a more primitive configuration than the tricuspid tooth form that is most common in Lancian and Recent species. The distribution of the Recent teiid genera is restricted to Central and South America with the exception of *Cnemidophorus,* which occurs in North America (e.g., Presch, 1974*a*). However, the fossil record of Teiidae indicates that the family probably originated sometime during the Early Cretaceous in North America, underwent a radiation in both North America and Central Asia during the Late Cretaceous, and then experienced a sharp decline in latest Cretaceous time. Ancestors of the nine Recent genera of the family (see Presch, 1983) may have invaded Central and South America sometime during the Late Cretaceous or Early Tertiary (Presch, 1974*a,* 1980, 1983; Estes, 1983*b*; Estes and Baez, 1985).

Early Cretaceous record.—The only known Early Cretaceous record of teiids is from the Comanchean of central Texas. Murry et al. (1989) reported the discovery of small tetrapods from the Twin Mountains, Glen Rose, and Paluxy formations (=Trinity Group). The description of this fauna was published by Winkler et al. (1990), in which several lizard jaws (SMU 72282, 72283, 72301) were referred to the family Teiidae (questionably subfamily Teiinae), but no identifications at generic and specific levels were attempted. These jaws show synapomorphies of the Teiidae such as extensive deposits of cementum around the tooth bases (see Winkler et al., 1990: fig. 6c) and a hypertrophied splenial, as indicated by the widely open Meckelian canal. In addition, other characters, such as the subpleurodont tooth attachment, well-developed subdental shelf and sulcus dentalis, are also indicative of the family Teiidae (Winkler et al., 1990). However, the teeth of these specimens are unicuspid (Winkler et al., 1990), suggesting to us that the unicuspid coronal pattern is primitive for the family (see above). According to Winkler et al. (1990), other jaws from the Comanchean of Texas resemble those of the Upper Jurassic paramacellodids (see Estes, 1983*a,* 1983*b*), indicating that the Comanchean materials may represent a transitional lizard assemblage between those of the Upper Jurassic and Upper Cretaceous.

Late Cretaceous record.—The Late Cretaceous was probably the most important interval for the early diversification of teiids (see Estes, 1983*a,* 1983*b*), as indicated by the fossil record from North America, the Gobi Desert, and possibly elsewhere in Asia (Fig. 6):

Uzbekistan: Nessov (1985, 1988) questionably assigned *Buckantaus crassidens* from the middle part of Taikarshin beds, Dzharakhuduk locality, Uzbekistan, to the Teiidae and identified other materials from the upper part of the Jalovatsh Formation, Kansay, as "small teiid-like lizards". Nessov (1988) claimed that the age of the Taikarshin beds is Coniacian and the Jalovatsh Formation is early Santonian. Both the assignment of these lizards to the Teiidae and the age of the beds are problematic, since the specimens are poorly preserved and the ages are

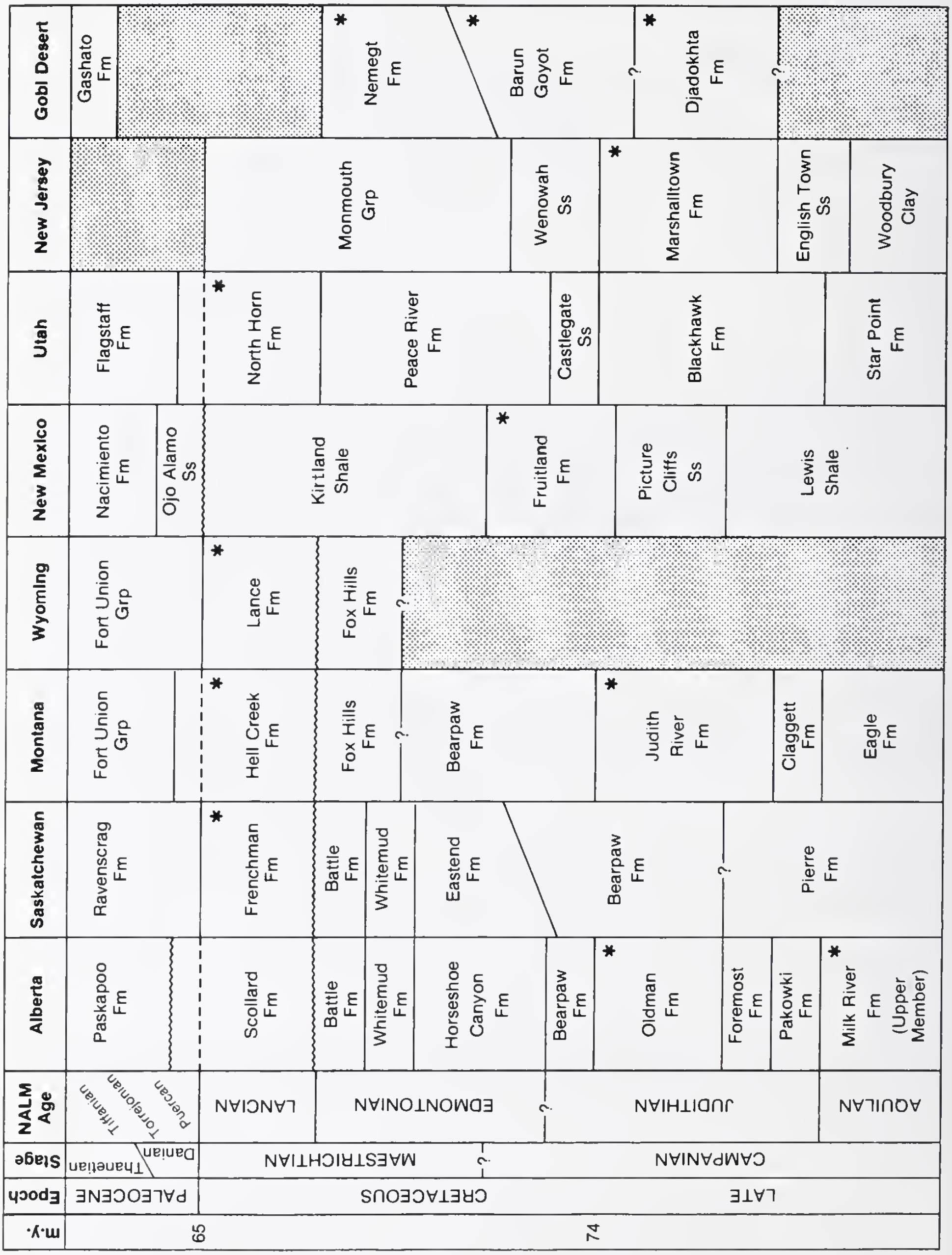

Fig. 6.—Chart showing Upper Cretaceous teiid-bearing formations (marked with "*") in North America and Asia.

based on sharks' teeth and brackish water molluscs, both unreliable biostratigraphically.

Mongolia: One of the largest collections of Mesozoic lizards is from the Upper Cretaceous of the central Asia Gobi Desert; since the 1920s, about 400 specimens, including skulls, jaws, and postcranial skeletons, have been collected from the Djadokhta Formation, from the Barun Goyot Formation, and from red beds in Khermeen Tsav equivalent to the Barun Goyot (see Sulimski, 1975), all of Campanian age (see, e.g., Fox, 1978; Lillegraven and McKenna, 1986). Teiid or teiid-like lizards are common in these collections. The following is a list of the Late Cretaceous teiids (*sensu* Estes, 1983*a*) known from the Mongolian Gobi Desert:

Macrocephalosaurus ferrugenous Gilmore, 1943
M. gilmorei Sulimski, 1975
M. chulsanensis Sulimski, 1975
Darchansaurus estesi Sulimski, 1975
Cherminsaurus kozlowskii Sulimski, 1975
Erdenetesaurus robinsonae Sulimski, 1975
Adamisaurus magnidentatus Sulimski, 1972

There is little consensus about the classification of these species at the familial level: Sulimski (1975) proposed the familial name Macrocephalosauridae to include the first four species in the list above, and used the name Polyglyphanodontidae (Gilmore, 1942) to include the next two species, plus three others from Utah (*Polyglyphanodon sternbergi, Paraglyphanodon utahensis,* and *Paraglyphanodon gazini*). Sulimski (1978) also proposed Adamisauridae for *Adamisaurus magnidentatus,* which he had earlier (1972) tentatively assigned to the family Agamidae. Estes (1983*a*) lowered the rank of Polyglyphanodontidae to subfamily (family Teiidae), and synonymized Macrocephalosauridae and Adamisauridae with Polyglyphanodontinae. His reasons for synonymizing these names can be summarized as: a) The twenty character states Sulimski (1975) used to separate Macrocephalosauridae and Polyglyphanodontidae as families are "almost entirely minor details of the sort generally used to separate species or genera" (Estes, 1983*a*:75); and, b) Sulimski's supposed eight diagnostic characters for the Adamisauridae either overlap with those of the Polyglyphanodontinae or are primitive, leaving the Adamisauridae indefensible as a separate taxon. In Estes' (1983*a*) view, *Adamisaurus* is an aberrant polyglyphanodontine. Additional specimens of *Adamisaurus* from the Upper Cretaceous of Inner Mongolia, China, are presently under study by the first author of the present paper and Prof. Hou Lianhai, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, and may provide further information about the relationships of *Adamisaurus.*

Sulimski (1984) named *Slavoia darevskii* on the basis of 46 skulls from the Barun Goyot Formation and Khermeen Tsav II, Gobi Desert. He provided no familial assignment of this lizard within the infraorder Scincomorpha, because "*Slavoia* is characterized by a mixture [of] characters occurring in various scincomorph families" (Sulimski, 1984:153). On the same page, however, he noted that *Slavoia darevskii* shows resemblances to some teiids and gymnophthalmids, and pointed out that a relationship with gymnophthalmids is the more likely; unfortunately, Sulimski (1984) did not specify the basis for this conclusion. Geographically, the Gymnophthalmidae (*sensu* Estes, 1983*a*; Presch, 1983) are presently restricted to South America, and lack a fossil record from South America or elsewhere (Estes, 1983*a*); Presch (1980) proposed a South American origin for the group. Thus, clarification of the relationship of *Slavoia darevskii* with other lizards is of importance; however, we know of no synapomorphies that might unite *Slavoia* with gymnophthalmids (see Estes et al., 1988:217).

North America: Late Cretaceous teiids from North America were first documented in the late 1800s. Marsh (1892) founded the name *Chamops segnis* on a fragmentary dentary (YUM 1036: this specimen is now housed in the U.S. National Museum of Natural History (Estes, 1983*a*)) and *Iguanavus teres* on several vertebrae from the "Laramie Formation" (=Lance Formation) of eastern Wyoming (the latter species name is the synonym of the former, according to Estes, 1964, 1983*a*). Marsh's naming of *Chamops segnis* also marked the first report of Late Cretaceous terrestrial lizards from North America.

The oldest record of North American Late Cretaceous teiids is of Aquilan or early Campanian age, from the upper member of the Milk River Formation (Russell, 1964; Williams and Burke, 1964): Fox (1972) was the first to recognize lizards of this age in North America and reported six lizard species in his preliminary list of the Milk River fauna; two of the six are definitely teiids. A detailed study of these lizards is being undertaken by the first author of the present paper.

The next oldest known record of Late Cretaceous teiids is of Judithian or mid-Campanian age. In addition to those from the Oldman Formation (see above), Sahni (1972) identified Judithian *Chamops segnis* and *Leptochamops denticulatus* from the Judith River Formation, Montana, and Parris and Grandstaff (1989) cited "teiids" as occurring in the Judithian Marshalltown Formation, New Jersey, although at this writing, these have yet to be described.

Late Campanian teiids are known from the Fruitland Formation, New Mexico (Armstrong-Ziegler, 1978, 1980; Sullivan, 1981). The late Campanian age of the Fruitland Formation has been determined from pollen (Fassett and Hinds, 1971), ammonite and radiometric dating (Cobban, 1973; Fassett, 1987; Brookins and Rigby, 1987), and comparison with Lancian and Judithian vertebrates from Wyoming, Montana, and Alberta (Armstrong-Ziegler, 1980; Lucas et al., 1987; Rigby and Wolberg, 1987). Armstrong-Ziegler (1978) recorded *Chamops segnis* and *Leptochamops denticulatus* together with anguid lizards in a faunal list; taxonomic descriptions of these lizards were published subsequently (Armstrong-Ziegler, 1980). Sullivan (1981) described an incomplete right dentary (UNM FKK-038a) from the Fruitland Formation, and identified the specimen as cf. *Chamops segnis.*

Another teiid, probably about the same age as those from the Fruitland Formation, is from Member B of the Wapiti Formation (Dawson, 1881; Allan and Carr, 1946), Kleskun Hills, near Grande Prairie, northwestern Alberta. Sternberg (1951) identified a fragmentary lower jaw (NMC 8891) from this horizon as *Chamops* cf. [*C.*] *segnis*; *C. segnis* is a common Lancian teiid. From the illustration (Sternberg, 1951:256), NMC 8891 seems to differ from the holotype (YUM 1036) of *C. segnis* and from the other specimens of this species that Estes (1964) described (UCMP 49871, 46033) in having relatively high crowned and less swollen teeth, as well as having a subdental shelf that sharply decreases posteriorly; NMC 8891 also retains the splenial. The age of the Wapiti Formation ranges from Campanian to Maestrichtian (Stott, 1975), whereas Member B of the formation is probably late Campanian (or somewhat younger) in age. Recent discovery of *Pachyrhinosaurus* (Ceratopsidae) fossils at Pipestone Creek (northwest Alberta) suggests that part of the Wapiti Formation correlates with the Horseshoe Canyon Formation (Edmontonian) of central Alberta (Tanke, 1988; Dodson and Currie, 1990).

The latest Cretaceous teiid record is late Maestrichtian or Lancian in age, from the Lance Formation, Wyoming (Marsh, 1892; Gilmore, 1928; Estes, 1964, 1983*a*); Hell Creek Formation, Montana (Estes, 1969; Estes et al., 1969); North Horn Formation, Utah (Gilmore, 1940, 1942, 1943; Clemens, 1961; Clemens et al., 1979; Lillegraven and McKenna, 1986); and Frenchman Formation, Saskatchewan (Fox, 1989). The following is a list of Lancian teiids presently known from North America (except for *Chamops* cf. [*C.*] *segnis,* which may be Edmontonian in age):

Polyglyphanodon sternbergi Gilmore, 1940
Paraglyphanodon utahensis Gilmore, 1940
Paraglyphanodon gazini Gilmore, 1943
Chamops segnis Marsh, 1892
Chamops cf. [*C.*] *segnis* (see Sternberg, 1951)
Leptochamops denticulatus (Gilmore, 1928)
Meniscognathus altmani Estes, 1964
Peneteius aquilonius Estes, 1969
Haptosphenus placodon Estes, 1964

All of the species listed above have been well described by previous authors, but the relationships of some are still unclear. The genus *Paraglyphanodon* is probably the closest form to *Polyglyphanodon* among Lancian teiids, as Gilmore (1943) originally recognized, although Estes (1969, 1983*a*) has noted that *Paraglyphanodon gazini* and *Paraglyphanodon utahensis* may be based on only young individuals of *Polyglyphanodon sternbergi.* A final decision about the validity of *Paraglyphanodon* must await a better understanding of ontogenetic changes in *Polyglyphanodon* (Estes, 1983*a*).

Possible relationships of *Chamops* with *Callopistes,* and *Peneteius* with Recent *Dicrodon, Teius,* and fossil *Paraglyphanodon* and *Polyglyphanodon,* have been discussed by Estes (1969, 1970, 1983*a*), as have those between *Leptochamops* and *Meniscognathus* with the Recent *Kentropyx-Cnemidophorus-Ameiva* group (Estes, 1964, 1983*a*). No evidence permitting more detailed interpretation has been discovered since. Estes (1983*a*) tentatively placed *Haptosphenus* in the subfamily Polyglyphanodontinae (Teiidae), but noted that this aberrant lizard may well be allocated to a different family in the future.

ACKNOWLEDGMENTS

Dr. D. A. Russell, National Museum of Natural Science, Ottawa, kindly allowed us to borrow NMC 13563 for study. We thank Zhang Jingfen for preparing the illustrations, and Asta Voss for sorting from screened concentrate the specimens for this research. We also acknowledge support for this research provided by graduate assistantships to Gao from the Department of Zoology, University of Alberta, and operating grants to Fox from the Natural Sciences and Engineering Research Council of Canada.

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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 2, Pp. 163–177 23 May 1991

FOSSIL CRABS (CRUSTACEA, DECAPODA) FROM THE MAASTRICHTIAN DIFUNTA GROUP, NORTHEASTERN MEXICO

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Abstract

Two species of fossil crabs have been collected from Maastrichtian deltaic deposits referred to the Potrerillos Formation of northeastern Mexico. *Mascaranada difuntaensis* is a new genus and species of carcineretid natatory crab. Morphological and paleoecological analysis suggest that the Carcineretidae is a heterogeneous group of reptant and natatory crabs whose taxonomy must be reconsidered. The fifth pereiopods of the natatory group are modified as in portunids, a family which may have descended from the carcineretids. The reptant forms may be more closely related to the Xanthidae. The youngest and southernmost occurrence of *Dakoticancer australis* Rathbun is recorded from two localities in the lower siltstone member of the formation. Twenty-four carapaces were found in two penecontemporaneous but paleoenvironmentally different localities. Most of the carapace remains are molts which, at one locality, were found associated with burrows, suggesting that this crab molted in burrows for protection. Some specimens are larger than previously reported for this species. Although this species is abundant in Mississippi Embayment *D. australis* Assemblages, it is an uncommon taxon in molluscan fossil assemblages at these Mexican localities. Biostratigraphic and paleobiogeographic ranges of *D. australis* are extended; the lower siltstone member or the Potrerillos Formation (Difunta Group) seems to be among the youngest Cretaceous crustacean-bearing units in North America.

Introduction

The Difunta Group is a terrigenous sequence of rocks comprising strata that range in age from Campanian to lower Eocene deposited in the Parras and La Popa basins in northeastern Mexico (Fig. 1) (Vega, 1987). The paleoenvironments interpreted for the Difunta units suggest the existence of two deltaic systems, whose progradation and local subsidence generated a cyclic lithologic sequence of chiefly siltstones, mudstones, and sandstones deposited in prodeltaic, delta front and marginal deltaic facies. Decapod crustaceans have been collected from several localities within the unit. It is the purpose of this paper to describe a new genus and species of carcineretid crab and to note the youngest and southernmost occurrence of *Dakoticancer australis* Rathbun from the Potrerillos Formation.

Although previous geologic work on the Difunta Group mentions some species of invertebrate fossils, the first paleontological report on the group was that of Wolleben (1977). He listed 52 species, including 1 coral, 13 gastropods, 28 bivalves, 7 cephalopods, 1 annelid, and 2 echinoderms. More recently, Vega and Perrilliat-Montoya (In press *a*) described the fossil molluscs collected in the lower siltstone member of the Potrerillos Formation within La Popa basin, recognizing

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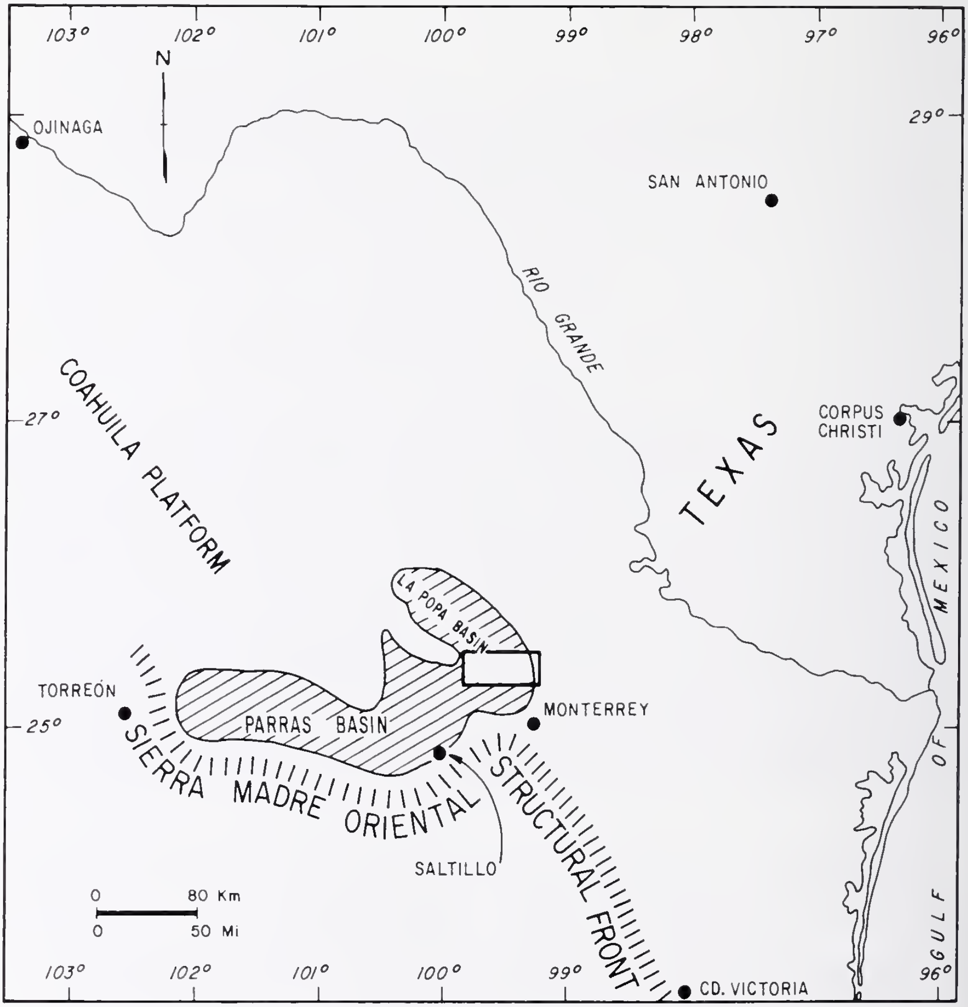


Fig. 1.—Geographic location map of Parras and La Popa basins (Difunta Group) in northeastern Mexico. Rectangle encloses area enlarged in Fig. 2.

17 species of gastropods, 20 bivalves, and five cephalopods. The fossil content of this member also includes crustacean carapaces and chelae. Vega and Perrilliat-Montoya (In press *b*) erected a new species of *Costacopluma* (Retroplumidae), a genus that had been reported previously from the Upper Cretaceous and Paleocene of western Africa (Collins and Morris, 1975).

A paleoecological analysis of the invertebrate fauna was made by Vega in an outcrop of the upper part of the lower siltstone member of the Potrerillos Formation near Las Ovejas Ranch, Municipio Mina, Nuevo Leon (Fig. 2, loc. B; IGM-1582). The lithology (mudstone and siltstone), scarcity of fauna, and lack of bioturbation, compared to the abundance and diversity of fossils in the basal coquinas, sandstones, and siltstones of the member, suggests a relatively deep-water environment in a lower delta-platform facies.

The lower siltstone member of the Potrerillos Formation contains *Exogyra* *costata* Say, and *Sphenodiscus pleurisepta* (Conrad), which are index fossils for the Maastrichtian of the Atlantic and Gulf Coastal Plain provinces (McBride et al., 1974; Cooper, 1971; Russell et al., 1982). On the basis of the stratigraphic range of several gastropod and bivalve species, Vega (1988) proposed that the lower siltstone member was deposited during the last three million years of the Maastrichtian, and concluded that the Cretaceous-Tertiary transition was preserved between the third and fourth members of the Potrerillos Formation (Fig. 3).

SYSTEMATICS

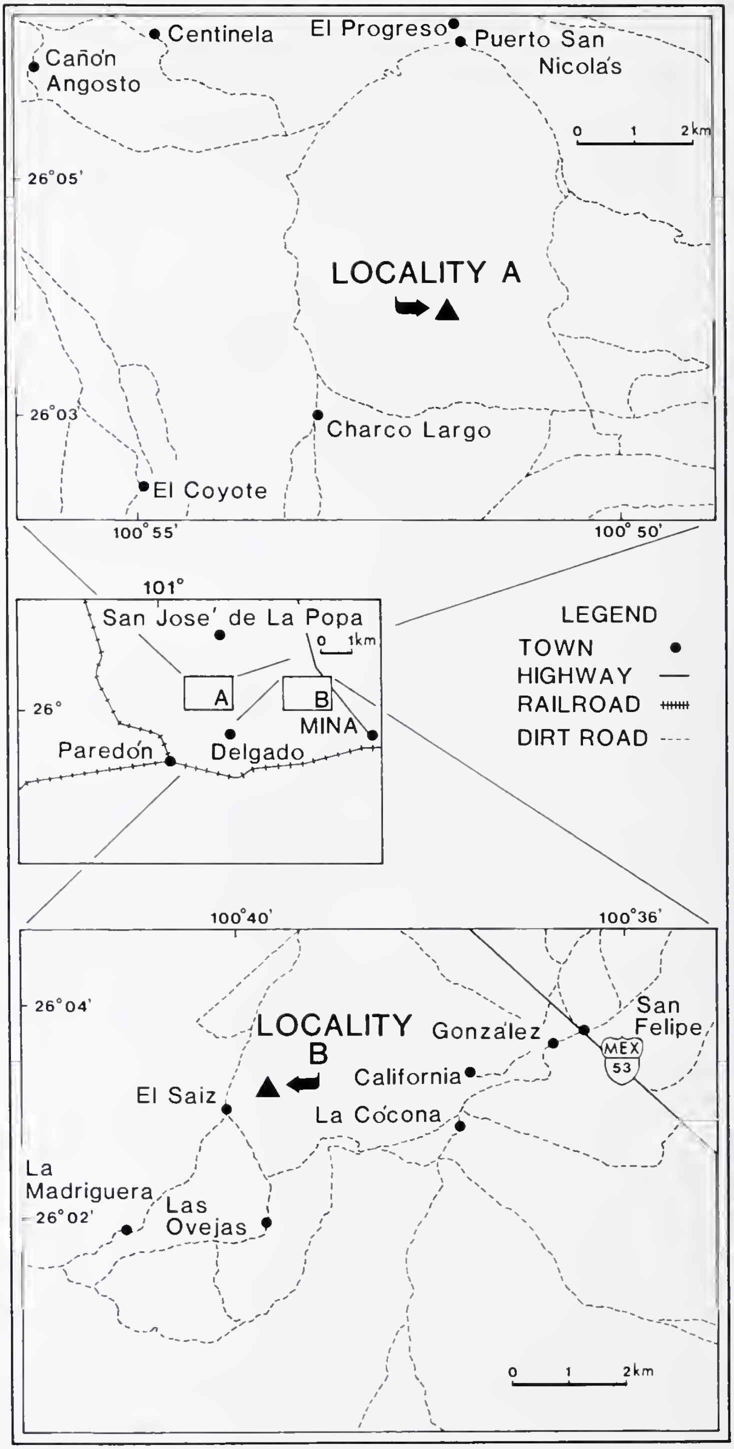
Order Decapoda Latreille, 1803
Infraorder Brachyura Latreille, 1803
Section Podotremata Guinot, 1977
Subsection Dromiacea Guinot, 1977
Superfamily Dakoticancroidea Rathbun, 1917
Family Dakoticancridae Rathbun, 1917
Genus *Dakoticancer* Rathbun, 1917

Type species.—Dakoticancer overanus by original designation (Rathbun, 1917).

Dakoticancer australis Rathbun, 1935
(Fig. 4, 5)

Dakoticancer overana: Rathbun *in* Wade, 1926.
Dakoticancer overanus: Glaessner, 1929.
Dakoticancer overana australis: Rathbun, 1935.
Dakoticancer overanus australis: Glaessner *in* Moore (ed.), 1969.
Dakoticancer australis: Bishop, 1983.
Dakoticancer australis: Bishop *in* Gore and Heck (eds.), 1986.

Description.—Carapace slightly longer than wide, semirectangular to oval longitudinally. About equally wide at levels of hepatic and branchial regions, slightly narrower at midlength. Carapace strongly vaulted; one specimen (IGM-5211) presumed not to be a molt, with a length of 41.5 mm, attains a height of 27.8 mm. Rounded ridges and relatively deep grooves differentiate carapace regions. Surface ornamented by conspicuous, coarse granules that cover all regions. Dorsal surface convex. Front downturned and narrow. Fronto-orbital margin ⅔ maximum width. Orbital margin defined laterally by small but conspicuous spine, with another smaller spine situated toward the rostrum at about midpoint of orbit; rostrum sulcate axially, downturned distally, laterally compressed at the base and widens downward. Anterolateral margin convex, continued posteriorly as nearly straight line. On lateral surface below hepatic and mesobranchial areas three fine ridges with granulated crests and three shallow furrows, last of which continues to abdominal region, project anteroventrally. Posterolateral margin curves abruptly to a short straight posterior margin which is nearly half of the maximum carapace width. Shallow marginal rim and furrow border posterior margin. Epigastric regions elongated posterolaterally on either side of rostral sulcus which is continuous with interior grooves defining epigastric regions. Epigastric and protogastric regions separated by posteriorly convergent grooves that disappear at frontal margin. Protogastric and mesogastric regions separated by shallow, longitudinal grooves that diverge posteriorly from rostral sulcus. Shallow grooves parallel to those between protogastric and mesogastric regions separate inflated protogastric and hepatic regions. Transverse cervical groove strongly convex an-


Centinela
El Progreso
Puerto San Nicolás
Cañón Angosto
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26°05'
LOCALITY A
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MINA
Paredón
Delgado
LEGEND
TOWN ●
HIGHWAY —
RAILROAD
DIRT ROAD ----
100°40'
100°36'
26°04'
LOCALITY B
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California
El Saiz
La Cócona
La Madriguera
26°02'
Las Ovejas
0 1 2km

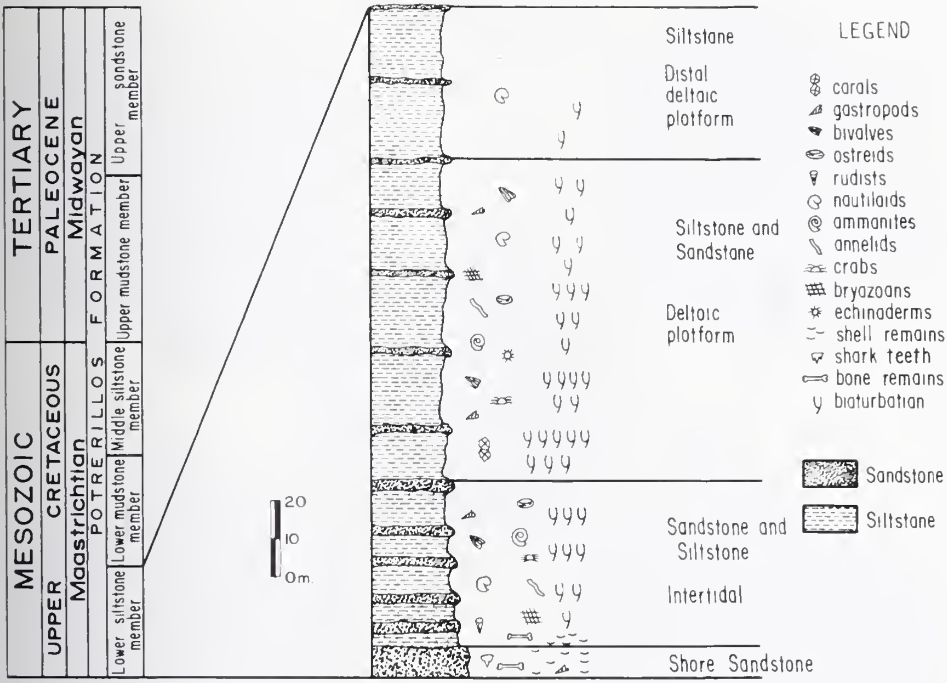

Fig. 3.—Stratigraphic section of the lower siltstone member of the Potrerillos Formation showing lithologic characteristics, faunal distribution and environmental interpretations.

teriorly, poorly defined or absent in axial region, delineates posterior margins of hepatic and protogastric regions, which are inflated posteriorly. Mesogastric and cardiac regions separated by lateral constriction of axial region and subtle sulcus. Longitudinal grooves continuous with cervical groove, interrupted by shallow pits at both sides of anterior portion of intestinal regions. A transverse groove, weakly convex anteriorly, separates mesobranchial and metabranchial regions but does not cross axial regions. Mesobranchial region strongly inflated, highest portion of carapace, as reniform ridge extending posterolaterally and decreasing in height toward lateral margin. Small, but prominent, boss projects axially at posteromesial corner. Metabranchial not as high as mesobranchial but with a central ridge that extends to the lateral margin, where it abruptly ends. Cardiac region slightly more elevated than metabranchial, and continuous posteriorly to lower and narrower intestinal region which is a shallow, inverted triangle terminating at level of metabranchial ridge. Pronounced slope extends to posterior margin. Sternal plastron well defined; triangular in shape, with granulated acute ridge near base of coxa of second pereiopod. Fourth to eighth thoracic sternites with transverse depressions and posterior granulated ridge. Eighth sternite small and subdorsal. Male sternum deeply and narrowly sulcate to near anterior termination.

←

Fig. 2.—Location map of the fossiliferous outcrops of the lower siltstone member of the Potrerillos formation where remains of *Dakoticancer australis* Rathbun and *Mascaranada difuntaensis* n. sp. were collected. Locality A (IGM-2444) lies at the northwest extremity of the Delgado syncline. Locality B (IGM-1582) is situated at the southwest side of La Zorra hill.

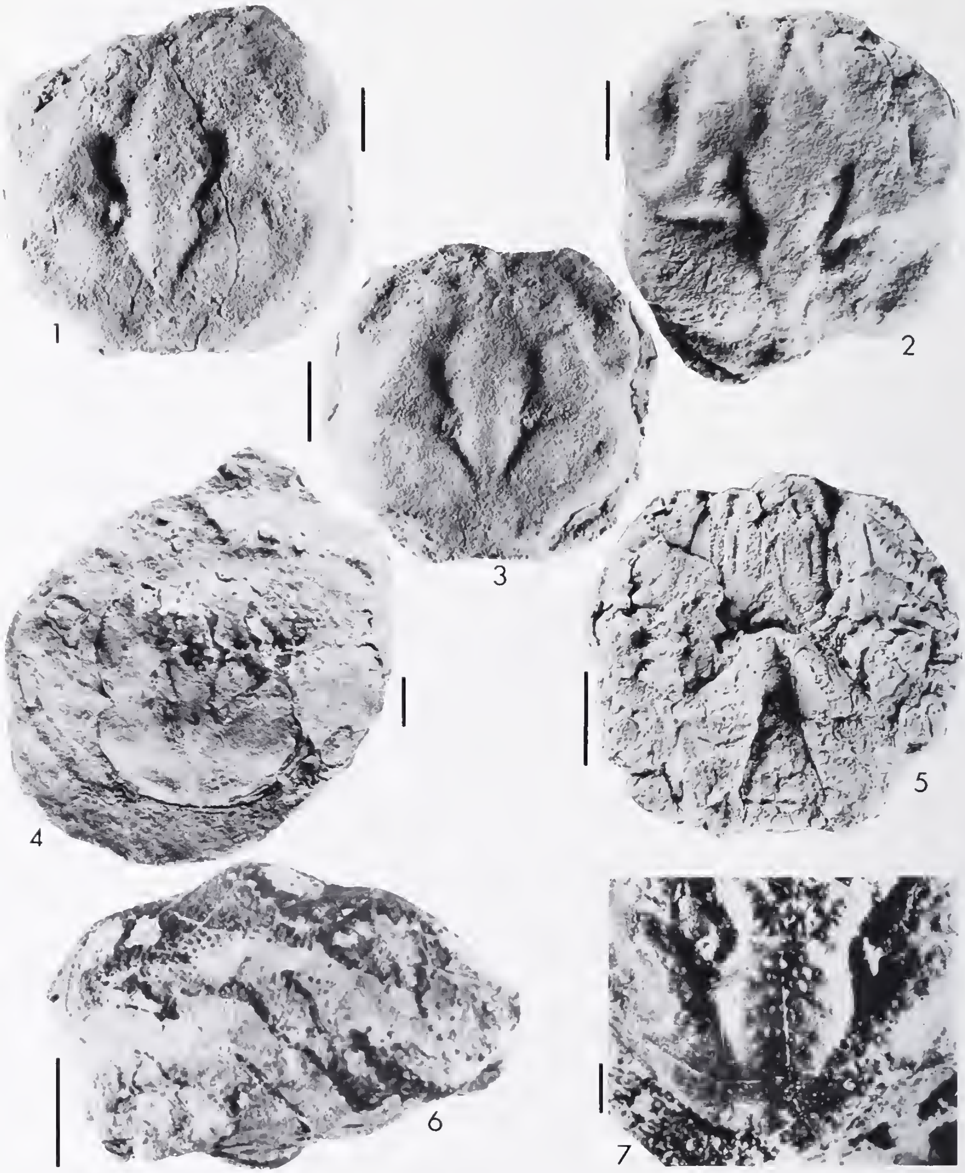

Fig. 4.—*Dakoticancer australis* Rathbun. Bar scales for figures 4.1–4.6 = 1 cm. Bar scale for figure 4.7 = 1 mm. 1, Dorsal view of carapace of largest specimen (IGM-5206) found in Difunta Group. Locality A. 2, Dorsal view of carapace showing details of fronto-orbital margin. Specimen IGM-5207, locality A. 3, Dorsal view of carapace showing details of posterior and posterolateral margin. Specimen IGM-5208, locality A. 4, Dorsal view of carapace with articulated appendages, included in a sandstone-filled burrow. Locality B. 5, Ventral view of carapace showing details of the sternum and buccal region. Specimen (IGM-5208). 6, Lateral view of right side of specimen IGM-5211, preserving carapace material, unwhitened. This specimen may not be a molt. Locality B. 7, Dorsal view of posterior portion of an incomplete juvenile specimen (IGM-5213). Locality A.

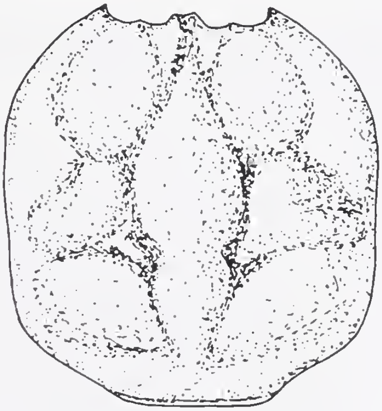

Fig. 5.—Line drawing of *Dakoticancer australis* showing the general disposition of body regions. The coarse pustulose ornamentation is not shown.

First abdominal somite subdorsal, crossed transversely by subtle granulate ridge. Second somite slightly wider than first, with well-marked transverse ridge that bears thick granules.

Buccal cavity nearly square. Small triangular notch in front of sternal plastron separates coxae and bases of third maxillipeds. Ischium of third maxillipeds long, rectangular and with pair of shallow furrows that extend longitudinally to subquadrate merus. Elongate, acute exognath on coxae of third maxilliped. Coxa-basis of first pereiopod inflated and with granulations. P2–P5 coxae-bases subtrapezoidal, centrally inflated and with low granules. Ischia not seen. Merus and cheliped stout and short, little compressed with strong granules and short spines on outer margin. Carpus shorter than merus but with strong granulations and spines; three strong ridges on upper surface. Palm with strong granulations and shallow grooves on its medial upper and lower surfaces. Moveable and fixed fingers not preserved. Pereiopods P2–P4 ambulatory, similar in size. Fifth pereiopod smaller than others and subdorsal.

A juvenile, incomplete specimen (Fig. 4.7) possesses nearly same posterior carapace morphology as do adults.

Hypodigm.—IGM-5206 to IGM-5213, deposited in the Museo de Paleontologia, Instituto de Geologia, Universidad Nacional Autonoma de Mexico; CM35511 to CM35514, in the Section of Invertebrate Paleontology, The Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Localities and stratigraphic position.—There are two principal outcrops of the lower siltstone member of the Potrerillos Formation where carapaces of *Dakoticancer australis* have been collected (Fig. 2). Eight molds of the interior and four molds of the exterior of carapaces were collected by Vega about 11.5 km southwest of San Jose de La Popa, at the margin of the Delgado syncline (Fig. 2, loc. A; IGM-2444). The same collector found nine molds of the interior with partial carapace material preserved, and three molds of the exterior, in an outcrop situated 21.2 km southeast of San Jose de La Popa, near the feature known locally as "La Zorra" hill (Fig. 2, loc. B; IGM-1582).

As is typical of deltaic deposits, the lower siltstone member undergoes lateral facies changes. Although the two localities where the material was collected are

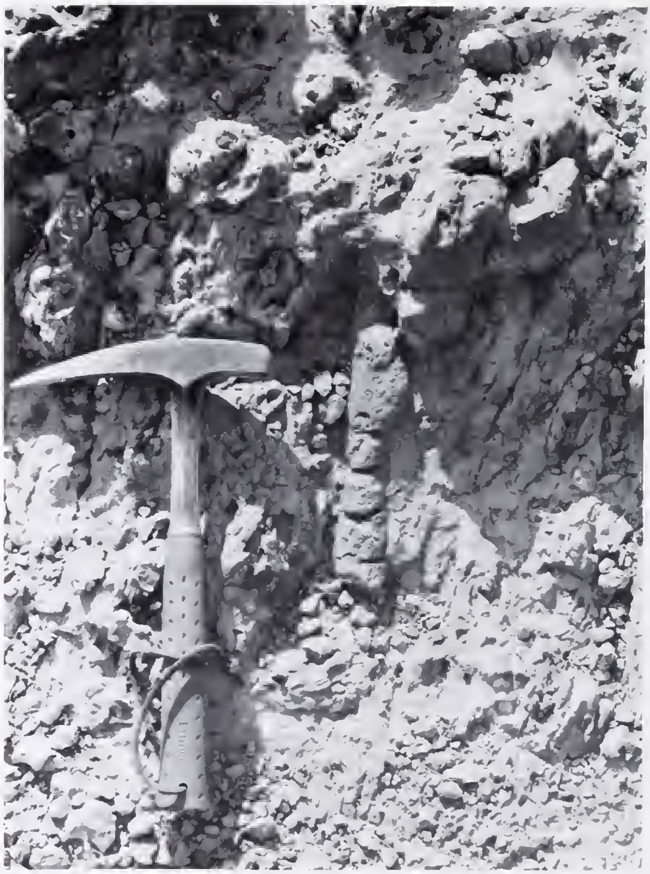

Fig. 6.—Outcrop of lower siltstone member at locality B. Note burrow where specimen IGM-5212 (Fig. 5.4) was collected.

situated at the same stratigraphic level, they represent different facies. Thus, preservational styles of the fossils are distinct. The molds of the interior found at locality A have lost the carapace material completely, and none was found with preserved appendages. This characteristic and the posterior displacement of the sternal plate suggests that these remains were molts deposited in a shallow environment. The matrix is a light-gray sandstone, which lacks bioturbation. In the same bed, two big chelae referrable to *Prehepatus* were collected. A bank that contains *Pycnodonte mutabilis* and *Exogyra costata,* with an approximate thickness of four meters, was located two meters above. This occurrence suggests that the molts may have been transported shoreward and filled with intertidal sandstone.

The lithology at locality B is finer-grained sediments, siltstones and mudstones, preserving a great diversity of molluscan species. Most of them are infaunal bivalves such as *Pholadomya* spp., and *Panopea* sp. Intense bioturbation with burrows filled with coarse brown sandstone (Fig. 6) is evident. Carapaces of *D. australis,* with appendages articulated (Fig. 4.4), were found in these burrows. Nevertheless, the carapaces show dislocation of sternal plates, which suggests that

Table 1.—*Measurements and computed ratios of Dakoticancer australis* Rathbun.

Specimen	Length (mm)	Width (mm)	W/L ratios
IGM-5206	54.0	53.1	0.98
IGM-5207	44.7	42.8	0.95
IGM-5208	40.3	37.5	0.93
IGM-5209	40.6	37.7	0.93
IGM-5210	39.1	37.6	0.96
			Mean = 0.95
IGM-5213[a]	9.3	9.1	0.98
Blue Springs, Miss.[b]	52.4	49.3	0.94
USNM F3840[c]	25.8	24.8	0.96

[a] The sole juvenile specimen collected from Nuevo Leon and the smallest member of the species collected to date.

[b] The largest specimen reported by Bishop (1986, p. 426, fig. 7).

[c] The holotype of *Dakoticancer australis* Rathbun.

these crabs molted while seeking haven in the burrows. This prevented transport and subsequent disarticulation of appendages. The exuviae were gradually filled by sand within the burrow during consolidation. This suggests a deeper environment than the one represented at locality A, in delta platform facies.

Measurements and condition of specimens.—The measurements reflecting the range of variation in size of specimens of *Dakoticancer australis* are given in Table 1. Those specimens with IGM numbers were collected from Nuevo Leon.

Although most of the molts lack carapace material, their preservation is adequate to describe the dorsal and ventral surfaces, as well as part of the chelipeds.

Remarks.—The specimens conform closely to the original description (Rathbun, 1935) and subsequent emendation (Bishop, 1983) of *Dakoticancer australis.* Rathbun (1935:40), referring to *Dakoticancer overana australis,* stated "This form differs from the typical one in the greater extent of the granulation of the carapace, the smooth areas restricted to narrow depressions between the elevations instead of covering their slopes as in the typical form. The carapace is narrower. The single rostrum is compressed at base and widens slightly toward the extremity. A female paratype (73840) measures 35.1 millimeters long from the orbital margin and 40 millimeters wide, or 1:1.14, whereas a typical *overana* (32056) measures 19.4:24.7 or 1:1.27." Bishop (1983:425) noted that *D. overana australis* tended to be subquadrate and had more strongly developed, shelf-like posterior intestinal and metabranchial regions. Furthermore, the claws were more oblique than those of *D. overanus overanus sensu* Rathbun. Bishop's (1983:425–426; fig.7) statistical treatment of *Dakoticancer overana sensu stricto* and *D. australis* indicated that the differences in carapace and claw morphology warranted specific distinction between the two taxa, a conclusion confirmed by a recent description of *D. overana* (Tucker et al., 1987).

The only other taxon that might be confused with *D. australis* is *Seorsus wadei* Bishop, 1988*b.* The latter is represented by only two partial molds of the interior. They appear to be more finely ornamented and have more convergent posterolateral margins than typical *Dakoticancer australis.* Otherwise, the two taxa are very similar with regard to the critical point of definition of regions. Certainly, whether or not *Seorsus wadei* represents a distinct genus, it certainly would appear to be a dakotacancrid.

Although most specimens of Nuevo Leon *D. australis* fall into the size range observed by Bishop (1983), at least four specimens are larger than those reported previously (Table 1). The sole juvenile specimen from the Nuevo Leon Assemblage is the smallest specimen of *D. australis* ever found (IGM-5213, Fig. 4.7). The Nuevo Leon Assemblage does not yield as many specimens as does the Coon Creek Formation where Bishop (1986) found 637 specimens.

This occurrence extends the paleogeographic range of *D. australis* southward from the Navarro Formation in Bexar County, Texas (Rathbun, 1935). The biostratigraphic range of *D. australis* is also extended from the middle Maastrichtian Prairie Bluff Formation (Bishop, 1986) to the late Maastrichtian lower siltstone member of the Potrerillos Formation.

Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Carcineretidae Beurlen, 1930
Mascaranada, new genus

Type species.—*Mascaranada difuntaensis,* new species.

Description.—Carapace subhexagonal to oval, 12% wider than long, widest part near midlength. Dorsal regions well defined by transverse, straight, finely granulated ridges and deep grooves. Rostrum very narrow. Anterolateral margin rounded, terminating in a fine extra-orbital spine; orbits narrow. Posterolateral margins straight, converging toward straight posterior margin, posterolateral corner gently curved. Protogastric region with well-marked transverse ridge that extends distally to cervical groove. Hepatic lobes with ridge which is oblique to orbital margin. Epibranchial lobes small, sinuous, ridged; mesogastric region forms inverted trapezoid, with transverse, straight, strong ridge. Branchial lobes well developed, semicircular in shape. Mesobranchial region broad, with strongly marked straight ridge extending to the carapace margin. Metabranchial regions nearly circular, domed, well defined. Cervical groove deepens and curves smoothly from margin toward axis and crosses axial regions as straight, narrow, deeply incised groove. Chelipeds not seen. Walking legs long (P2–P4); fifth pereiopod with flattened propodus and oval dactylus.

Etymology.—The generic name combines two Spanish words, *mascara,* mask and *nadar,* to swim. The pattern of regions, ridges, and grooves on the carapace of this swimming crab resembles a primitive mask.

Comparison.—The regions, which are well defined by grooves and transverse ridges, the shape of the frontal margin, and the form of the fifth pereiopods are characteristic of the Upper Cretaceous family Carcineretidae, which contains the following genera: *Carcineretes* Withers, 1922; *Cancrixantho* Van Straelen, 1934; *Lithophylax* Milne Edwards and Brocchi, 1879; *Ophthalmoplax* Rathbun, 1935; *Woodbinax* Stenzel, 1952; *Longusorbis* Richards, 1975; and *Icriocarcinus* Bishop, 1988*a*. Bishop recognized "two natural groups" within the Carcineretidae (1988*a*: 247). The first group includes those species with a U-shaped carapace, straight lobed fronts, and bilobed rostra, including *Ophthalmoplax, Woodbinax,* and *Carcineretes.* Those species with pentagonal or subhexagonal carapaces, with similar areolation and more or less well-developed transverse ridges, spiny or lobed fronts, and narrow non-bifurcated rostra comprise the second group. *Cancrixantho, Longusorbis, Icriocarcinus,* and probably *Lithophylax* are referrable to this group.

Although the shape of the carapace and transverse ridges suggests that the affinities of *Mascaranada* are with Bishop's second group, the new genus lacks areolation, and the fifth pereiopods are natatory, in contrast with the ambulatory ones

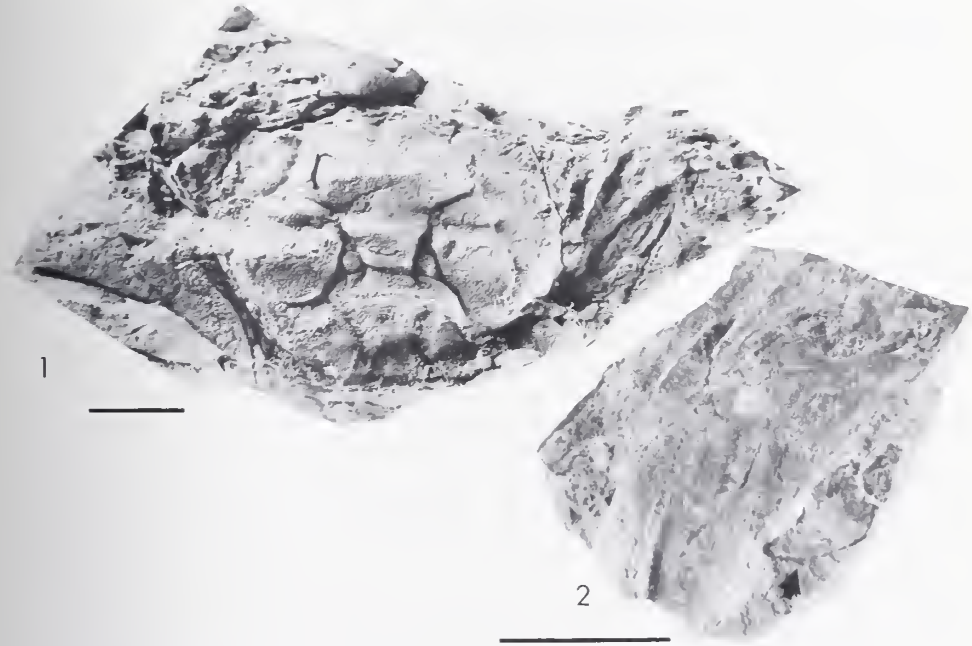

Fig. 7.—*Mascaranada difuntaensis.* 1, Dorsal view of carapace of holotype IGM-5204 (× 1.9). 2, Fifth left pereiopod (arrow) with flattened propodus and oval dactylus. Same specimen (× 3.3). Locality IGM-1582).

of *Longusorbis* (Richards, 1975:1858), and *Icriocarcinus* (Bishop, 1988*a*:251). *Cancrixantho* differs from *Mascaranada* in having much wider and spinier frontal and posterolateral margins. *Lithophylax* is small, has a narrower marginal front, less-pronounced transverse ridges, and stronger pereiopods. Whether *Mascaranada* is a member of Bishop's first group is also unclear. The lack of areolation, and the presence of natatory fifth pereiopods, are morphological characteristics that suggest that *Mascaranada* is related to Bishop's first group. However, the urn-shaped carapace of *Ophthalmoplax,* its lateral spines, and short posterior margin readily distinguish this genus from *Mascaranada. Woodbinax* is smaller, has a straighter anterior margin, and better defined anterior portion of the mesogastric area. Thus, *Mascaranada* exhibits some morphologic characters of both groups, which may suggest that differentiating between the two groups is not possible.

Mascaranada difuntaensis, new species
(Fig. 7, 8)

Description.—Carapace subhexagonal to oval, 12% wider than long. Widest part at level of epibranchial lobes, arched longitudinally and straight transversely; highest in center, with deep grooves and strong transverse ridges. Fronto-orbital margin narrower than the maximum width, sinuous in form. Frontal area narrow, defined laterally by short, well-defined preorbital spines. Central part of frontal margin with elongated granulations. Orbital margin a curved ridge terminating laterally at distinct postorbital spines directed anteriorly and axially. Anterolateral margins broadly rounded, merging with straight, steeply inclined posterolateral margins. Posterolateral corners sharply rounded; posterior margin straight, nar-

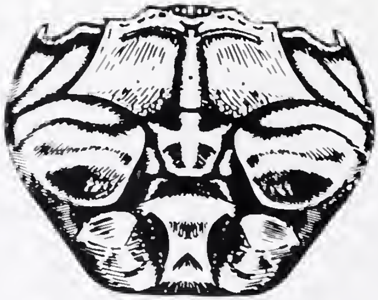

Fig. 8.—Line drawing of *Mascaranada difuntaensis* carapace (× 1.8).

row, about same width as frontal region. Carapace grooves rather broad, clearly differentiating regions. Protogastric area crossed by transverse ridge with three nodes, one central and the others situated 3.9 mm on either side of midline. Transverse ridges somewhat reduced axially, and decreased laterally. Mesogastric region an inverted trapezoid, continuous with obscurely marked narrow extension that vanishes before reaching front. Central part of mesogastric region with strong transverse ridge that marks maximum height of carapace. Hepatic lobes relatively narrow, well differentiated from protogastric and epibranchial lobes by shallow groove that curves from inner orbital margin to anterolateral corner at point of origin of cervical groove. Epibranchial lobes narrow and transverse, slightly inclined toward mesogastric region, delimited anteriorly by cervical groove, and posteriorly by groove that deepens axially. Cervical groove arched, attaining maximum depth along margin of axial regions, continuous from lateral margin to midline. Mesobranchial lobe subrectangular with a strong medial transverse ridge that reaches margin near point of maximum carapace width. Urogastric area inclined, subtrapezoidal and separated by a short but very deep groove from mesogastric region. Branchial lobes semicircular, well differentiated as prominent tubercles near deepest part of cervical groove. Cardiac region with distinct transverse ridge and pronounced slope that reaches posterior margin; intestinal region indistinct. Metabranchial areas narrow, circular, domed on line with transverse ridge on cardiac region. Crests of ridges with granulations.

Pereiopods P1–P4 ambulatory, and fifth pereiopod with flattened propodus and paddle-like dactylus (Fig. 7.2). Ventral and frontal carapace surfaces and chelipeds not seen.

Holotype.—IGM-5204, deposited in the Museo de Paleontologia, Instituto de Geologia, Universidad Nacional Autonoma de Mexico.

Locality and stratigraphic position.—The holotype was collected from the upper portion of the lower siltstone member (upper Maastrichtian) of the Potrerillos Formation (Fig. 3), at the base of Cerro La Zorra, Municipio Mina, Nuevo Leon, approximately 50 km northwest of Monterrey, in a canyon known regionally as Cañon de Potrerillos (Fig. 2, loc. B: IGM-1582).

Measurements and condition of specimen.—Carapace length 29.6 mm; width 35.1 mm. The height cannot be measured, as the abdominal region is covered. The holotype of the new species described here was found nearly complete, and is interpreted to be a mold of the interior. When collected, the fifth pereiopod exhibited a portunoid form with a flattened propodus and oval dactylus. Erosion has damaged the anterolateral portions of the carapace and parts of the appendages were broken during collecting. The left pereiopod was rescued. Although the preservation of the specimen is good, the fragile nature of the matrix precludes cleaning of the abdominal region.

Etymology.—The trivial name refers to the Difunta Group, which seems to yield the most diverse Cretaceous brachyuran fauna known from Mexico.

Comparison.—*Mascaranada difuntaensis* superficially resembles *Ophthalmoplax brasiliana* (Maury), from the Upper Cretaceous of Brazil (Beurlen, 1958) in the distribution and shape of the deep grooves and transverse ridges and in the natatory nature of the fifth pereiopods. However, *O. brasiliana* is larger (L, 85–99 mm; W, 102–120 mm; Beurlen, 1958:8) and has long spines on the distal portions of the frontal margin. The urogastric region seems to be longer and the cardiac shorter than in *M. difuntaensis.* The illustration of *O. brasiliana* by Maury (1930:4, fig. 1) shows a rectangular carapace, much wider than long, with posterolateral spines. *Ophthalmoplax stephensoni* Rathbun is more nearly square and has a small spine on the anterolateral margin. The shape of the frontal margin is similar to that of *M. difuntaensis. Ophthalmoplax stephensoni* also has three prominent nodes in the middle part of the protogastric ridge (Rathbun, 1935). Description of *O. comancheensis* Rathbun is based on dactylus shape, but the general carapace form in all species of *Ophthalmoplax* differs from that of *Mascaranada.*

Phylogeny and paleoecology.—Glaessner (1969:R440) stated, "The origin of the Portunoidea, . . . was sought near the Cancridae because of their resemblance with the Carcininae. These were thought to be primitive compared with the advanced Portuninae and the aberrant Podophthalminae. The available fossils show that the history of crabs adapted for active swimming is more complicated, and they could even be polyphyletic . . . The Cretaceous Carcineretidae are unlike typical xanthids. They have a number of advanced portunoid characters, such as adaptation of the fifth pereiopod (where known) for swimming, transverse ridges on the carapace. . . ." *Mascaranada difuntaensis* has the typical characters of the Carcineretidae, including swimming adaptations that suggest relationship to the Tertiary Portunidae. Some of the representatives of Bishop's second group, for example *Longusorbis cuniculosus* Richards, were found associated with burrows in lowest-tide level facies (Richards, 1975:1857) and on muddy bottoms, below wave base (Bishop, 1988*a*:246). It seems that this group inhabited shallow waters, burrowing for protection, as reptant crustaceans. Representatives of the natatory group could crawl and swim in deeper waters, as none was found associated with burrows. A lower delta-platform facies was interpreted to be the environment of deposition for the siltstones and mudstones at the type locality. There was no evidence of bioturbation or of transport of the specimen, as articulated appendages were preserved. *Mascaranada difuntaensis* was probably an active crawler and swimmer on the deltaic platform of this portion of the ancestral Gulf of Mexico. It also seems that the paleogeographic distribution of the natatory group, consisting of *Ophthalmoplax, Carcineretes, Woodbinax,* and *Mascaranada difuntaensis,* was restricted to the Gulf Coast and Caribbean provinces, while the members of the reptant group mainly inhabited the Pacific Slope Province (Bishop, 1986). This distributional pattern also tends to ally *M. difuntaensis* to Bishop's first group. He has previously (1986) suggested that the Cretaceous crabs of North America exhibit a high degree of provincialism. If this separation of groups is correct, the shape of the fifth pereiopod could be the basis for subdivision of the Carcineretidae. The natatory forms may be the ancestors of the Portunidae, which are distinguished from the remaining Heterotremata on the basis of the natatory modifications of the fifth pereiopod. Another possibility might be inclusion of the reptant Carcineretidae in the Xanthidae.

ACKNOWLEDGMENTS

We thank Jose Luis Villalobos, Departamento de Carcinologia, Instituto de Biologia, UNAM, for his comments to the senior author on morphology and paleoecology. Mr. Antonio Altamira, Laboratorio de Fotografia, Instituto de Geologia, illustrated the material. Mr. Luis Burgos provided several sketches of the fossils. Mayra Lizzet Gonzalez provided invaluable help reviewing the manuscript. Parts of this paper were criticized by Luis Chirino-Galvez, Calvin Frye, Dale Tshudy and Annette Tucker, Department of Geology, Kent State University. Financial support for fieldwork was given by the Instituto de Geologia, Universidad Nacional Autonoma de Mexico. Contribution 456, Department of Geology, Kent State University, Kent, Ohio 44242.

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4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 60 4 SEPTEMBER 1991 NUMBER 3

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ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

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ANNALS OF CARNEGIE MUSEUM

Vol. 60, Number 3, Pp. 179–210 4 September 1991

THE RHYSODINI OF AUSTRALIA (INSECTA: COLEOPTERA: CARABIDAE OR RHYSODIDAE)

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Abstract

The Rhysodini known from Australia are illustrated and described and keys are provided. Sloanoglymmiina, new subtribe, and *Sloanoglymmius,* new genus, are proposed for *Rhysodes planatus* Lea. The following new species are described (type localities indicated): *Kaveinga* (*Angekiva*) *stiletto* (Queensland, Lamington National Park); *Kaveinga* (*Angekiva*) *walfordi* (Queensland, 29 km southeast of Mareeba); *Rhyzodiastes* (*Rhyzoarca*) *ovicollis* (Queensland, Ramsay's Scrub, Cooloola); *Omoglymmius* (*Caeconavitia*) *okei* (Queensland, Blue Mountains, Cape York Peninsula); *Omoglymmius* (*s. str.*) *bituberculatus* (Queensland, Boar Pocket); *Omoglymmius* (*s. str.*) *monteithi* (Queensland, West Claudie River, Iron Range). The Australian fauna contains 13 species in five subtribes, five genera and eight subgenera.

Intraspecific variation, distributions within Australia, and zoogeographic relationships with other regions are given. Rhysodini are restricted to the forests along the east coast, including nearby mountains from Cape York to Tasmania. *Sloanoglymmius* is taxonomically isolated and shares only plesiomorphic characters with *Leoglymmius.* Both are restricted to Australia. *Omoglymmius* (*Caeconavitia*) previously thought to be endemic to Fiji, has a species in northern Queensland. Otherwise, the new taxa do not alter the picture of Australian rhysodine zoogeography as presented in previous papers.

Introduction

The Rhysodini is a moderate-sized group of beetles which has commonly been placed in the suborder Adephaga as an independent, presumably primitive family. Bell and Bell (1962) disagreed, concluding to the contrary that it should form a tribe Rhysodini within the Carabidae. The Rhysodini represents a lineage of ground beetles which is highly modified for life within rotten wood, and for a specialized diet, presumably slime molds. At the present, the position of the group is still being debated.

We (Bell and Bell, 1978, 1979, 1982, 1985) have monographed the world fauna at the species level, and a fifth part is in preparation on the phylogeny and zoogeography of the group. However, we have previously treated the Australian fauna only superficially, since we had not seen the type specimens housed in Australia, and had studied only the limited material which had found its way into European and North American museums. A sabbatical leave (1988–89) allowed us to study the Australian species in the same detail as those of other continents, as well as to assess the zoogeographic relationship of the Australian species.

Rhysodini, in general appearance, resemble Carabidae of the tribe Scaritini, especially *Clivina.* They are similar in shape, and often in size and color. Rhysodini are easily separated from all other Carabidae by the presence of a deep median pit, often connected to a system of grooves, on the dorsal surface of the head.

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Submitted 21 June 1990.

Additional features include differentiation of a narrow, condyliform "neck", fusion and elongation of the mentum so that it conceals the remaining mouthparts in ventral view, and presence in males of "calcars", anteriorly directed processes on the apices of the hind, and usually also the middle tibiae. The calcars are absent in females, and thus are a reliable means of identifying the sexes. Since all known Rhysodini look red-brown in bright light and piceous to black if seen in dimmer light, color descriptions have been omitted.

Rhysodini are limited to forested regions where there is sufficient rainfall to permit the decay of wood and the growth of slime molds. In general, they are absent from forests which have a strongly marked dry season. In Australia they seem to be restricted to wet or at least moderately wet sclerophyll and rain forest. They are difficult to find and collect. The most fruitful collection method involves the prying apart of suitable logs, stumps or roots with a screwdriver, small crowbar or similar instrument. At times, machetes, hatchets or saws are useful. Some species have been found in dead spots in recently fallen branches of live trees, in major roots as deep as three meters below the surface, or in rotten areas in the centers of large standing trees. *Rhyzodiastes mirabilis* is usually found on small sticks in forest litter (G. B. Monteith, personal communication, 1989).

Rhysodini are often gregarious, although seemingly less so in Australia. If a single specimen is found within a log, a careful dissection of the log will often reveal a large number of specimens. It is sometimes practical to take an entire log back to the laboratory for systematic searching. Members of different species have been found in the same log.

Fully-winged species are, on rare occasions, collected at light traps and flight intercept traps. This is especially likely if the trap is in forest. Some of the vestigial-winged species have been taken in pitfall traps in forest litter or in Berlese samples. There is evidence that the beetles occur on the surface of logs during or after thunderstorms.

The larvae are found in short tunnels within rotten wood. The tunnel is filled in behind the larva by wood chips, evidently cut by the larva as it extends the tunnel. The larvae have leg segmentation typical of suborder Adephaga, but the body is soft, without distinct sclerites, and the urogomphi are absent. Each body segment, or most of them, has a dorsal transverse "comb" of stout spiniform setae.

Abbreviations used in the text are: ANIC, Australian National Insect Collection, Canberra, ACT; BMNH, British Museum (Natural History), London; BPM, Barry P. Moore, private collection, Canberra, ACT; BSRI, Biosystematics Research Institute (now called Biosystematics Research Center), Ottawa; CAS, California Academy of Sciences, San Francisco; CSIRO, Commonwealth Industrial and Scientific Research Organization, Canberra, ACT; DPIB, Department of Primary Industries, Brisbane; LUN, Zoological Institute, Lund, Sweden; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MMUS, Macleay Museum, Sydney; MNHN, Muséum National d'Histoire Naturelle, Paris; MVIC, Museum of Victoria, Natural History, Abbotsford, VIC; QM, Queensland Museum, South Brisbane; QPIM, Department of Primary Industries, Mareeba, QLD; QUIC, University of Queensland Insect Collection, St. Lucia, QLD; SAMA, South Australian Museum, Adelaide; TM, Transvaal Museum, Pretoria; UVM, University of Vermont, Zoology Department, Burlington, Vermont; L/GW, ratio of pronotal length divided by its greatest width; ACT, Australian Capitol Territory; NSW, New South Wales; QLD, Queensland; TAS, Tasmania; VIC, Victoria.

GLOSSARY

Apical striole—a short fragment of a stria on the outer face of the apical tubercle of the elytron, appearing as a curved row of punctures arising from the marginal stria and curving back toward it distally.

Apical tubercle—an elevated region along the lateral margin of the elytron near the apex, bounded medially by the subapical impression.

Discal striole—a more or less linear anterior extension of the basal impression of the pronotum.

Frontal groove—one of a pair of grooves extending anteriorly from the frontal space, separating the median lobe from the temporal lobes.

Frontal pit—a deep depression in the dorsal surface of the head between the temporal lobes, concealed partially by the tip of the median lobe and medial angles of the temporal lobe.

Frontal space—the visible external opening of the frontal pit, bounded anteriorly by the median lobe, laterally by the temporal lobes and limited posteriorly by the medial angles of the temporal lobes.

Inner carina—the elevated ridge lying between the median groove and one of the paramedian grooves of the pronotum.

Intercalary stria—the stria laterad the parasutural stria and medial to the subapical tubercle. This terminology is used in the tribe Clinidiina where there is reduced striation.

Intratubercular stria—in Clinidiina, the stria laterad the intercalary stria, if present. It can be identified by the fact that its apex passes between the subapical and apical tubercles.

Minor setae—a group of many short setae on the antennal segments, shorter and more numerous than apical or basal setae. They are generally distributed on the cone of segment XI, but on the more proximal segments they may be grouped either as a broad irregular band (Fig. 4), a single row in an encircling subapical ring (Fig. 5) or an isolated tuft (Fig. 3).

Orbital groove—a groove on the lateral margin of the temporal lobe, just medial to the upper edge of the eye, often appearing as a posterior continuation of the antennal groove.

Outer carina—the elevated ridge between the paramedian groove and the marginal groove of the pronotum.

Parafrontal boss—an isolated convex, glabrous area lateral to the median lobe.

Paramedian groove—a groove extending from the anterior to posterior margin of the pronotum about halfway between the median groove and the lateral margin, separating the inner and outer carinae.

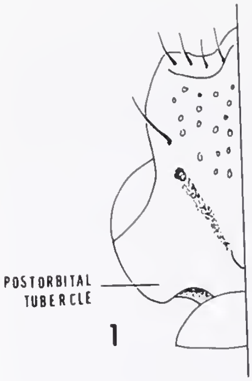
Parasutural stria—the stria laterad the sutural stria and mesad the intercalary stria as defined in the Clinidiina.

Postorbital tubercle—(Fig. 1) a prominence on the posterior side of the head, directly posterior to the eye.

Stylet—a needle- or chisel-like structure at the tip of antennal segment XI (Fig. 3).

Subapical tubercle—a tubercle mesad the apical tubercle of the elytron and separated from it by the intratubercular stria in the Clinidiina.

Suborbital tubercle—a prominence on the posterior surface of the head, ventrad the eye, best seen in lateral view.



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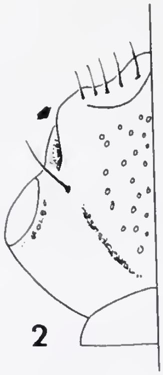

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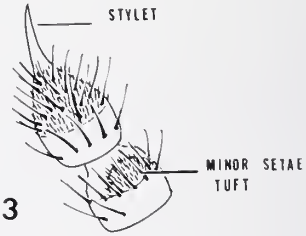

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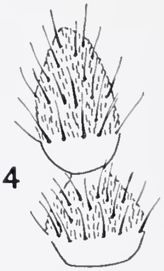

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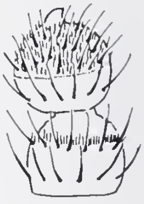

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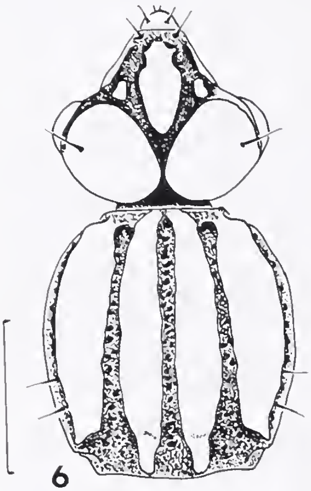

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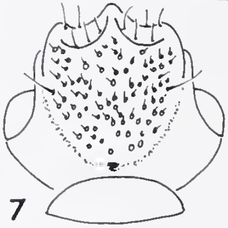

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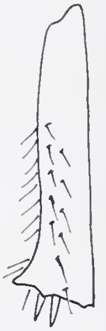

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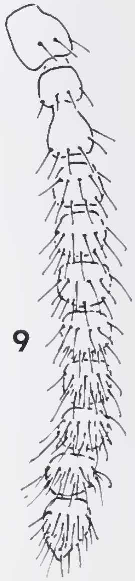

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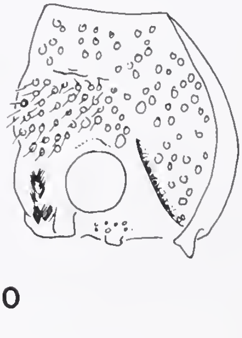

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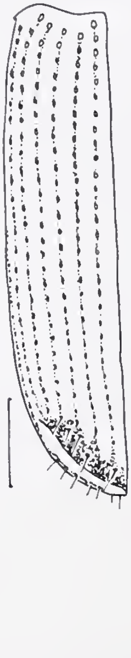

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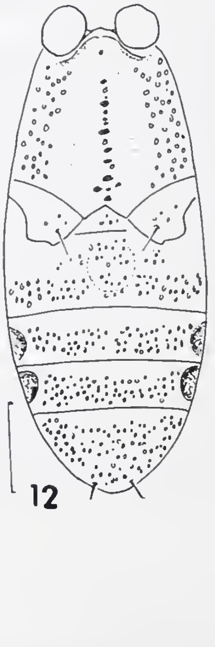

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SYSTEMATICS

Seven subtribes are now known. Five of these occur in Australia. As the remaining two subtribes are from the Southern Hemisphere, and either of them might be found in Australia in the future, all are included in the key below.

Key to Subtribes of Adult Rhysodini

1. Mentum separated laterally from gena by a cleft (Fig. 2) 2

1′. Mentum completely fused laterally to gena (Fig. 1) 3

2.(1.) Minor setae of outer antennal segments in broad bands (Fig. 4); pronotum with paramedian grooves narrow, complete; median groove with anterior, posterior pits; pronotum much narrower than elytra; elytral humerus not dentate .... Leoglymmiina

2′. Minor setae of outer antennal segments forming subapical ring on each segment (Fig. 5); pronotum with rounded basal impressions, without paramedian grooves; median groove linear, not expanded at either end to form anterior, posterior median pits; pronotum broad, almost as wide as elytra; elytral humerus dentate .... Sloanoglymmiina, new subtribe

3.(1′.) Minor setae of outer antennal segments forming a tuft on ventral side of segment (Fig. 3) or minor setae entirely absent (except apical segment) .... Clinidiina

3′. Minor setae of each outer antennal segment forming a subapical ring (usually only one seta in width) (Fig. 4) 4

4.(3′.) Median lobe of head elongate, extending to neck constriction, widely separating temporal lobes .... Rhysodina

4′. Median lobe not so elongate, not separating temporal lobes 5

5.(4′.) Median lobe not defined; frontal pit round, porelike; frontal grooves absent or barely suggested (Africa, South America, New Zealand) .... Dhysorina

5′. Median lobe defined by frontal grooves, usually deep 6

6.(5′.) Frontal pit absent; median grooves very shallow, meeting at neck constriction (South Africa) .... Medisorina

6′. Frontal pit present, overhung by tip of median lobe; frontal grooves deep in most species; if grooves are very shallow, then frontal pit is large, crescentic .... Omoglymmiina

Subtribe Leoglymmiina

Type genus.—*Leoglymmius* Bell and Bell, 1978.

Description.—Minor setae of antennal segments V–X forming broad band encircling distal third of each segment; segment XI without antennal stylet (Fig. 9); median head lobe short, convex with distinct parafrontal boss on either side; temporal lobes convex, oval, strongly convergent posteriorly; eye large, circular; cleft present between mentum and gena (Fig. 2).

⟵

Fig. 1–2.—Head, right ventral aspect, diagrammatic: Fig. 1. Showing complete fusion of mentum and gena; Fig. 2. Arrow showing position of cleft between mentum and gena. Fig. 3–5.—Antennal segments X–XI, diagrammatic, showing position of minor setae. Fig. 6–12.—*Leoglymmius lignarius* (Olliff): Fig. 6. Head, pronotum, dorsal aspect; Fig. 7. Head, ventral aspect; Fig. 8. Hind tibia, male; Fig. 9. Antenna; Fig. 10. Prothorax, left ventrolateral aspect; Fig. 11. Left elytron, dorsal aspect; Fig. 12. Metasternum, abdomen, ventral aspect, female.

Paramedian grooves of pronotum complete, linear, curved, coarsely punctate (Fig. 6); prosternum densely setose near middle (Fig. 10); elytral striation complete, stria VII marginal; apical striole absent; apex of elytron with broad, opaque, flattened, densely microsculptured area, but without distinct subapical impression, since apical tubercle is poorly defined (Fig. 11); metasternum with broad punctate area along each lateral margin and line of punctures along midline; abdominal punctures numerous, shallow, in broad bands; lateral pits present on sterna IV, V, shallow, subequal in female (Fig. 12), obsolete in male; middle, hind tibiae (Fig. 8) each with two nearly equal spurs.

This subtribe contains a single genus and species, endemic to Australia.

Leoglymmius Bell and Bell, 1978

Type species.—*Rhysodes lignarius* Olliff, 1885, by original designation.

Leoglymmius lignarius (Olliff, 1885)

Rhysodes lignarius Olliff, 1885:471.

Type specimen.—Lectotype (here designated) male, labelled "*Rhysodes lignarius* Olliff, Lambing Flat" [near Yass, N.S.W.] (ANIC on permanent loan from MMUS).

Rhysodes blackburnii Grouvelle 1903:117, synonymized by Moore (1987).

Type specimens.—Lectotype (designated by Bell and Bell, 1979), male, labelled "Victoria, Australia" (MNHN). Paralectotypes: one female, same data as lectotype (MNHN); one male labelled "doit provenir d'Australie" (MNHN).

Rhysodes trichosternus Lea 1904:81, synonymized by Moore (1987).

Type specimen.—One assumed syntype, sex not recorded, labelled "Victoria" (SAMA), not studied by us.

Diagnosis.—Distinguished by the suture separating gena and mentum, broad bands of minor setae on outer antennal segments, absence of apical tubercle and indistinct basal scarp on elytron.

Description.—Length 8.1–9.7 mm. As indicated for subtribe; additional characters described by Bell and Bell (1979); male genitalia figured (Bell and Bell, 1978). The labrum is shield-shaped and has a minute pair of setae near the midline on the anterior margin, in addition to the usual large pair on the dorsal surface. Bell and Bell (1979) erroneously stated that there is only one pair of labral setae. Mentum (Fig. 7) with tiny setae in punctures, more numerous in females.

Distribution.—Forested regions of the southern two-thirds of New South Wales (from Barrington Tops, south), ACT, VIC and TAS. The geographic distribution suggests that this species is more tolerant of dry conditions than are other Rhysodini (Fig. 74, Map B).

Localities.—ACT: Boboyan Rd., 1 km N/Grassy Creek, 23 Dec 1979 (ANIC); Brindabella Mts, Blundells Cr. Rd., Nov 11, 1988, in eucalyptus log (UVM); Naas Ck, near Mt. Clear, 2 Nov, 1980 (ANIC). NSW: Barrington Tops N. Pk., 5000 ft, Feb 8, 1932 (MCZ); Mt. Canabolas, 3500–4000 ft 7 Nov. 1987 (ANIC); Cabramurra, 3-ii-1962 (BPM); Clyde Mt., 6-IV-1980 (BPM); Hampton, no date (ANIC); Monga, 11-I-1978 (BPM); Kiandra, 9-2-52 (MVIC); Macquarie Pass, 23 Dec. 1953 (MVIC). TAS: Hobart area, 20-VIII-1986, in firewood (BPM); previously reported from Hobart by Lea, 1904. VIC: Echo Flat, 27-XII-1962 (BPM); Belgrave, 20-8-32 (BPM); same locality, 21-6-36 (MVIC); Grampians, Apr 1957 (MCZ); Sherbrooke Forest, Aug. 27–31, 2000 ft (MCZ); Bendoc, Jan. 1938 (MVIC); Macedon, 15-2-49 (MVIC); Ballarat, 5-11-08 (MVIC); Warneet, Jan. 1912 (MVIC); Olinda, 19-5-40 (MVIC); Trafalgar (MVIC); Mt. Hotham, c. 6000 ft Apr. 57 (ANIC); The Gap Scenic Reserve, S/Bonang, Jan. 15, 1989 (UVM).

Subtribe Sloanoglymmiina, new subtribe

Description.—Minor setae of antennal segments V–X in circle; segment III about twice as long as II or IV; basal and apical setae present; apical setae on segments I–XI, basal setae on segments V–X; segment XI without apical stylet (Fig. 16); median head lobe shield-shaped, notched by anterior tentorial pits; temporal lobes convex, closest together just posterior to tip of median lobe, evenly rounded posteriorly; frontal grooves narrow; frontal pit small; orbital groove extends posteriorly to posterior margin of eye, latter large, round; labrum broad, semicircular, with one pair of setae; one temporal seta; anterior part of gena separated from mentum by slit (best seen in lateral view); small setae present on mental punctures, more prominent in males (Figs. 14, 17).

Pronotum relatively broad (L/GW 1.03), basal width nearly equal to that of elytra; lateral margin sharply defined, limited by distinct lateral "bead" (less rounded than in other Rhysodini, and more like that of other tribes of Carabidae); apex narrowed; lateral margin sinuate anterior to hind angle; latter rectangular; marginal groove (or bead) with two or three lateral and one angular setae, latter slightly anterior to angle; median groove linear, without either anterior or posterior pit; both marginal and median grooves finely punctate; basal impressions wide, rounded anteriorly without any hint of discal strioles (Fig. 13); prosternum densely punctate except near anterior margin (Fig. 20).

Elytron (Fig. 19) wlth seven striae; elytra relatively short, humerus forming sharp angle; striae fine, punctate, regular except striae I and II, each of which has double row of punctures near apex (suggesting each results from the fusion of two striae); apical striole with single row of punctures anteriorly, becoming scattered band several punctures wide posteriorly; striae effaced at base; apical tubercle and subapical depression slightly developed, depression densely punctate; stria I with 1–2 setae near apex; stria II with 3–4 setae near apex; stria IV with 4–6 evenly-spaced setae from base to apex; subapical tubercle with three setae; stria VII with 3–4 setae near apex (Fig. 19); metasternum, abdomen densely, shallowly punctate; both sexes with round pits near lateral margins of sternum IV, pit larger in female (Fig. 18); metepimeron slightly lobate, more distinct than in other Rhysodini.

Middle, hind tibiae each with two nearly equal spurs; male with middle calcar pointed; hind calcar subacute, very small (Fig. 15).

This subtribe has one genus and species, endemic to southeastern Australia.

Sloanoglymmius, new genus

Type species.—Rhysodes planatus Lea, 1904, here designated.

Description.—As for subtribe.

Etymology.—This genus is named for Thomas Sloane, pioneer Australian coleopterist, whose work in carabid phylogeny was ahead of its time, and has not been sufficiently appreciated.

Sloanoglymmius planatus (Lea), new combination

Rhysodes planatus Lea, 1904:82.

Type specimen.—Holotype (sex not determined), labelled "Victoria" (SAMA).

Yamatosa planata Moore, 1987:22.

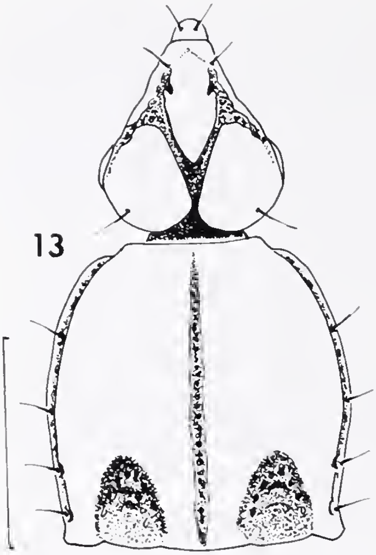
Diagnosis.—Distinguished by the suture separating gena from mentum, minor setae of antennal segments V–X in single ring, pronotum with deep round basal impression without discal striole, 4–6 setae on stria IV.

Description.—Length 7.2–8.2 mm, as for subtribe.

Distribution.—From the vicinity of Canberra (Brindabella Range and Mt. Clyde) south into Victoria (Fig. 74, Map C).

Localities.—ACT: Blundells Ck. Rd., 3.5 km E/Piccadilly Circus, 24 Oct. 1982 (ANIC); same locality and date (TM); same locality, Nov. 18, 1988 (UVM). NSW: Clyde Mt., 29 Jan. 1975 (ANIC); Clyde Mt., 6-IV-80 and 31-XII-78 (BPM); Monga S. For., Dec. 14 & 28, 1988 (UVM). VIC: Belgrave, 2-4-49 (MVIC); Whittlesea, Sep. 1944 (MVIC).

Remarks.—This genus resembles *Yamatosa* Bell and Bell and *Dhysores* Grouvelle in the absence of paramedian grooves; however, the presence of a distinct cleft between the mentum and the gena excludes it from those genera, and is a symplesiomorphy shared with *Leoglymmius.* The arrangement of the minor antennal setae separates it from the latter genus. Both genera are best placed in



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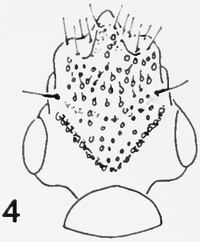

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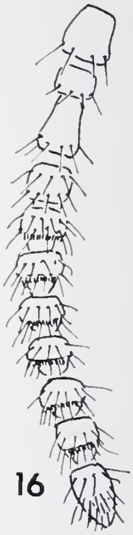

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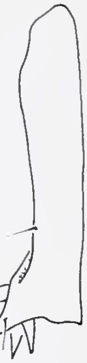

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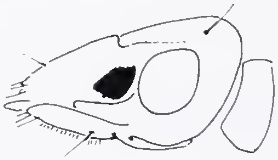

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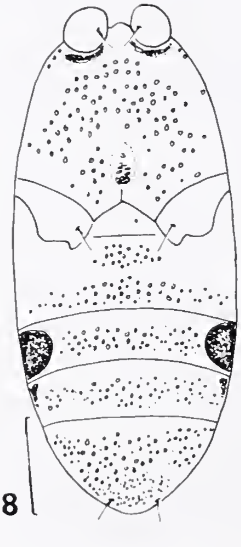

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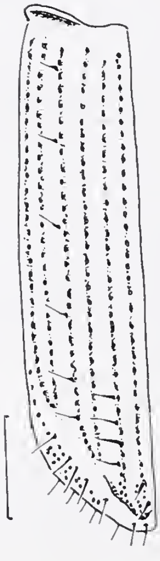

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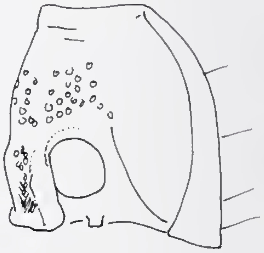

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monotypic subtribes, and each has features closer to those of more normal Carabidae than do other rhysodines. *Leoglymmius* is the more plesiomorphic in the distribution of minor antennal setae, while the plesiomorphic feature of *Sloanoglymmius* is seen in the sharp pronotal margin with well-defined lateral bead.

Subtribe Rhysodina Bell and Bell, 1978

Type genus.—Rhysodes Dalman, 1823 (Palearctic).

Description.—Minor setae of each outer antennal segment in a subapical ring; median lobe of head elongate, extending posteriorly over neck condyle, temporal lobes therefore widely separated; mentum fused to gena laterally; elytron with seven striae; middle tibia of male without calcar; hind tibia with small calcar, one spur.

Distribution.—New Zealand, New Caledonia, Australia, west to Mindanao and Celebes, and Palearctic from Japan to Europe. One of the three genera occurs in Australia.

Kaveinga Bell and Bell, 1978

Type species.—Rhysodes abbreviatus Lea, 1904.

Description.—Median lobe not sublinear; humeral tubercles distinct. For a more extensive description see Bell and Bell (1979).

Distribution.—Mindanao and Celebes through New Guinea to Santa Cruz islands and New Caledonia, south to New Zealand, Australia and Tasmania. Two of the four subgenera are found in Australia.

Key to Australian Subgenera of Adult Kaveinga

1. Paramedian grooves linear, slightly sinuate; pollinosity of paramedian grooves largely or entirely limited to punctures .... *Angekiva* Bell and Bell

1′. Paramedian grooves broad, deep, entirely pollinose, not visibly punctate .... *Kaveinga* sensu stricto

Subgenus *Angekiva* Bell and Bell, 1979

Type species.—Rhysodes frontalis Grouvelle, 1903.

Description.—Antennal stylet present or absent; antennae not pollinose; median groove of pronotum coarsely punctate; paramedian grooves more or less curved, linear except at extreme base, complete, coarsely to sparsely punctate, pollinosity restricted to punctures or nearly so; angular seta present or absent; marginal seta absent; prosternum coarsely punctate, punctures either generally distributed or restricted to margins of precoxal carinae; elytral striae glabrous; femora glabrous, middle tibia without lateral serrulation or lateral setae.

Distribution.—Endemic to eastern Australia from northern Queensland to Tasmania.

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Fig. 13–20.—*Sloanoglymmius planatus* (Lea): Fig. 13. Head, pronotum, dorsal aspect; Fig. 14. Head, ventral aspect; Fig. 15. Hind tibia, male; Fig. 16. Antenna; Fig. 17. Head, left lateral aspect; Fig. 18. Metasternum, abdomen, ventral aspect, female; Fig. 19. Left elytron, dorsal aspect; Fig. 20. Prothorax, left ventrolateral aspect.

Key to Adults of Species of Subgenus Angekiva

1. Antenna with apical stylet; both sexes with ventral tooth on anterior femur; angular seta at or very near hind angle of pronotum, the angle distinct .... *Kaveinga stiletto,* new species
1′. Antenna without apical stylet; femoral tooth absent in female, present or absent in male; angular seta either displaced anteriorly or absent; hind angles rounded 2
2.(1′.) Marginal groove of pronotum nearly complete; angular seta present, displaced anteriorly; male with profemoral tooth .... *Kaveinga frontalis* (Grouvelle)
2′. Marginal groove absent; angular seta absent; male without profemoral tooth .... *Kaveinga walfordi,* new species

***Kaveinga* (*Angekiva*) *stiletto*, new species**

Type specimens.—Holotype male, labelled "Lamington N.P., 28. 14S-153.08E, (O'Reilly's) Q, 22–27 Oct. 1978, Lawrence & Weir" (ANIC). Paratypes: QLD: one male, 2 females, same data as holotype (ANIC); one male, one female, same locality as holotype, 2–4 March, 1980, J.F. Lawrence (ANIC); one male, Nat. Park, Q, McPherson Rge., Mar. 1932, 3–4000 ft Darlington (MCZ); one female, Lamington Binna Burra, 16-11-82, Endrödy-Younga (TM); 2 females, Lamington Nat. Prk., ii-1964, G. Monteith (QUIC), 5 males, 5 females, same locality & collector, 4-IX-1966 (QUIC); one female, Lamington Nat. Prk., 23-V-62, T. Brooks (QUIC), same locality, one female, 23-5-45, A. Gardner, one male, 14–20:2:1958, I. C. Yeo (both QUIC); one male, one female, Bald Mt. area via Emu Vale, 3–4000 ft, 22–27-i-1971, D.L. Hancock (QUIC); one female, Emu Vale, 25-7-23, no coll. (QUIC); one male, Cunningham Gap, 24-i-1966, B. Cantrell (QUIC); one male, Tamborine Mt., 17-iii-1964, G. Monteith (QUIC); one male, Mt. Glorious, 3-IV-1966, B. Cantrell (QUIC); one female, 2 undet. gender, MacPherson Rge., 1923 (DPIB); one male, one female, Levers Plateau via Rathdowny, 22-IV-67, B. Franzmann (DPIB); one male, Emu Vale, 25-7-33, #3640 (DPIB); one male, one female, Mt. Tamborine, E. Sutton (MVIC); 2 females (same mount), Mt. Tamborine (SAMA). NSW: one male, Richmond River (MNHN); one female, N/Dunoon, Apr. 58, Darlingtons (MCZ); one male, one female, Bruxner Park, 200 m, Coffs Harbor, Jul 1978, S. & J. Peck (ANIC); one male, Brindle Ck., 800 m.nr. Kyogle, Wiangaree S.F., 20 Jun 78, S. & J. Peck (ANIC); one male, Wiangaree S. For., 600 m, Sheepstation Ck., 29-ii–3-iii-1980, A. Newton & M. Thayer (ANIC); one male, Dorrigo N.P., 700 m, ii Jul 1978, S. & J. Peck (ANIC); one male, one female, Carrai Plateau via Kempsey, 3-5-1967, G. Monteith (QUIC); 2 females, Tooloom Plateau via Woodenbong, 30-XII-1966, G. Monteith (QUIC); 2 females, Illawarra, H. W. Cox, H. S. Carter, 20-4-22 (MVIC); one male, Comboyne, H. S. Carter, 20-4-22 (MVIC); 2 males, Richmond River (SAMA). Also one female labelled "E.W. Ferguson", no locality (ANIC) and one female labelled "Qld., Nat. Park, Jan. 1928, Nicholson" (ANIC).

The last two specimens were labelled as *R. lignarius* Olliff by Lea, and the Richmond River specimen from MNHN was so labelled by Grouvelle, accounting for the fact that the true *R. lignarius* (now in *Leoglymmius*) was renamed by both of these authors.

Etymology.—This species derives its name from the presence of the acute stylet on antennal segment XI which is unique for the genus *Kaveinga.*

Diagnosis.—Distinguished by the acute stylet on antennal segment XI; angular seta at or near hind angle of pronotum; temporal lobes separated by long, nearly parallel-sided median lobe of head.

Description.—Length 5.8–7.4 mm; antennal segment XI with small, conical, acute stylet (Fig. 26); ring of minor setae present on antennal segments VI–X; basal setae on segments VI–XI; median lobe of head relatively narrow, margins nearly parallel; parafrontal bosses sharply separated from median lobe; well-defined orbital groove extending to posterior margin of eye; one large temporal seta (Fig. 21); eye large, oval; labrum pointed, with one pair of setae; mentum with two pairs of major setae (Fig. 22).

Pronotum rather elongate; L/GW 1.16; lateral margins slightly sinuate anterior to hind angles, latter nearly rectangular; median groove narrow, punctate; paramedian grooves complete, vaguely punctate; marginal grooves complete; angular seta present, located very near hind angle (Fig. 21); prosternum with precoxal carinae; prosternum, propleuron with coarse, relatively sparse punctures, glabrous except for pollinosity near anterior margin (Fig. 23).

Elytron with one seta near apex of stria IV, several in depression at apex of stria II and one on subapical striole, approximately eight in apical portion of stria VII; metasternum, abdomen coarsely punctate, female with small lateral pit on sternum IV (Fig. 24); both sexes with ventral tooth on anterior femur; hind calcar small, slightly bent upwards (Fig. 25).

Distribution.—Subtropical forest of southern Queensland and coastal New South Wales from Mount Glorious, north of Brisbane, to vicinity of Sydney (Illawarra) (Fig. 74, Map B).

Kaveinga (*Angekiva*) *frontalis* (Grouvelle)

Rhysodes frontalis Grouvelle, 1903:104.

Type specimen:—Holotype male, labelled "Tasmania" (MNHN).

Kaveinga frontalis: Bell and Bell, 1978:59.
Kaveinga (*Angekiva*) *frontalis*: Bell and Bell, 1979:394.

Diagnosis.—Distinguished by the broad median lobe of head which separates temporal lobes; anterior displacement of angular seta of pronotum, oval shape of pronotum; four labral setae.

Description.—Length 5.1–7.6 mm; antennal segment XI without apical stylet; complete rings of minor setae on segments VI–X; basal setae present on segments VI–XI; labrum with four (two pairs) of setae; median lobe of head relatively broad, narrowest at level of anterior margin of eye, dilated posteriorly; parafrontal bosses at least narrowly connected to median lobe; temporal lobes rounded, narrowly separated from median lobe; orbital groove well defined but short, ending opposite middle

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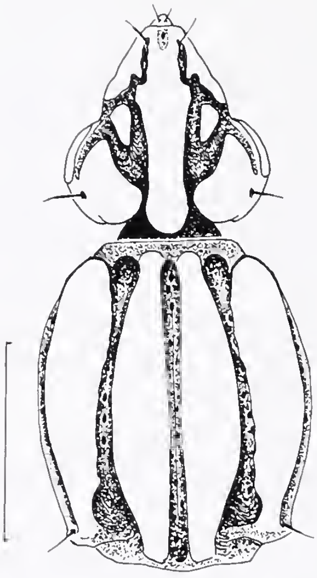
Fig. 21–26.—*Kaveinga* (*Angekiva*) *stiletto,* new species: Fig. 21. Head, pronotum, dorsal aspects; Fig. 22. Head, ventral aspect; Fig. 23. Prothorax, left ventrolateral aspect; Fig. 24. Metasternum, abdomen, ventral aspect, female; Fig. 25. Hind tibia, male; Fig. 26. Antenna. Fig. 27–32.—*Kaveinga* (*Angekiva*) *walfordi,* new species: Fig. 27. Head, pronotum, dorsal aspect; Fig. 28. Head, ventral aspect; Fig. 29. Head, left lateral aspect; Fig. 30. Prothorax, left ventrolateral aspect; Fig. 31. Metasternum, abdomen, ventral aspect, female; Fig. 32. Hind tibia, male.

Fig. 33–37.—*Kaveinga* (*Angekiva*) *frontalis* (Grouvelle): Fig. 33. Head, pronotum, dorsal aspect; Fig. 34. Prothorax, left ventrolateral aspect; Fig. 35. Metasternum, abdomen, ventral aspect, female; Fig. 36. Hind tibia, male; Fig. 37. Head, left lateral aspect. Fig. 38–41.—*Kaveinga* (*Kaveinga*) *abbreviata* (Lea): Fig. 38. Head, pronotum, dorsal aspect; Fig. 39. Metasternum, abdomen, ventral aspect, female; Fig. 40. Hind tibia, male; Fig. 41. Left elytron, dorsal aspect.



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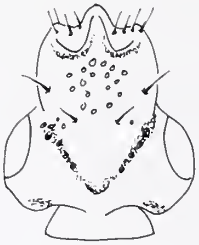

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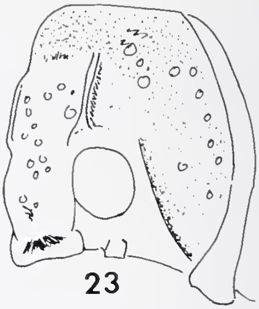

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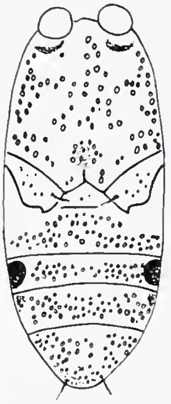

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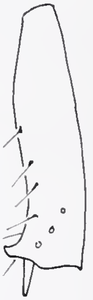

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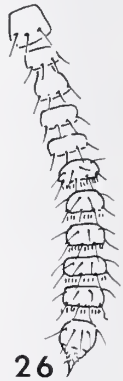

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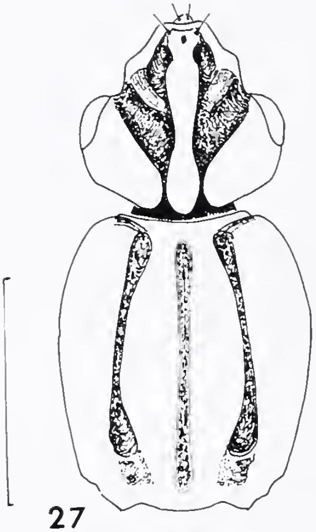

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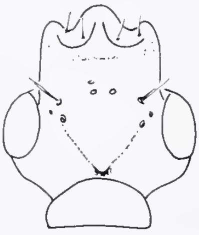

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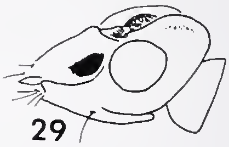

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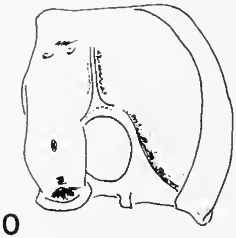

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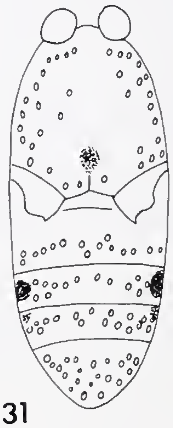

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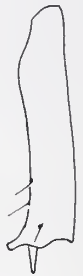

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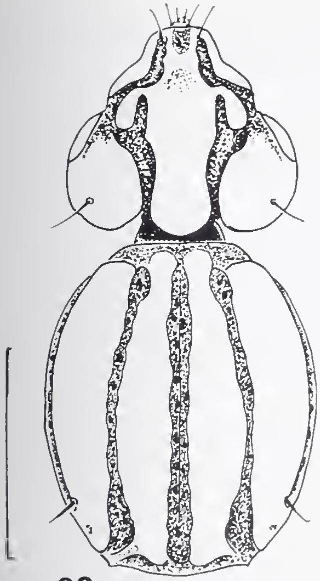

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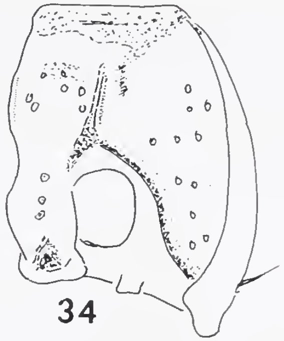

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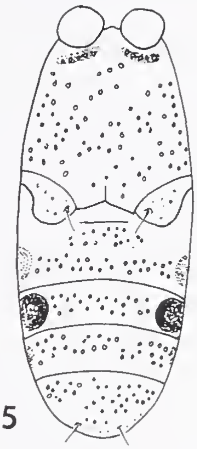

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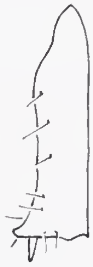

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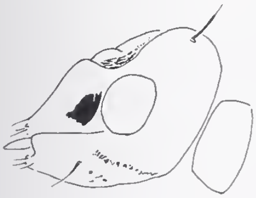

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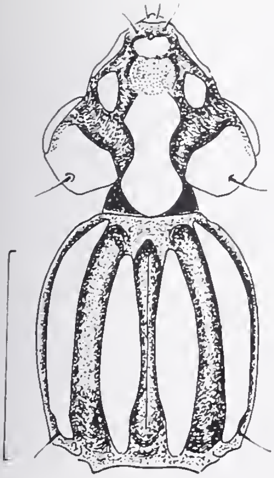

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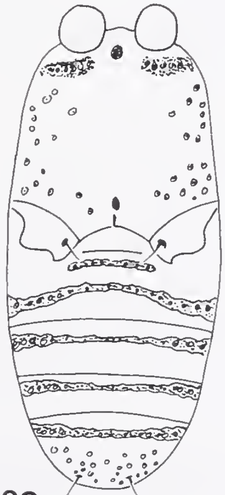

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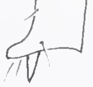

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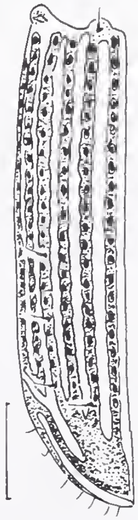

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of eye; one temporal seta located posterior and medial to orbital groove (Fig. 33); eye moderately large, oval (Fig. 37) becoming pigmented in some, probably older specimens (our erroneous report [Bell and Bell, 1979] that the eye is reduced was based on the holotype, which has it almost completely obscured by pigment); mentum with one pair of major setae.

Pronotum elongate, L/GW 1.18; lateral margins strongly curved, base scarcely wider than apex; lateral margin not sinuate posteriorly, hind angles scarcely distinct; median groove narrow, punctate, dilated at anterior pit, slightly so at posterior pit; paramedian grooves complete, punctate, dilated into small pits at anterior ends, and into narrow basal impressions at posterior ends; marginal groove nearly complete, but ended posteriorly at angular seta, which is displaced anteriorly about 15% of pronotal length; small pit present between angular seta and pronotal base (Fig. 33); prosternum with precoxal carinae; prosternum, propleuron with coarse, rather sparse punctures, glabrous except along anterior margin (Fig. 34).

Elytron without setae in subapical impression, with 1–2 in apex of stria IV, none on apical striole, approximately four in apex of stria VII; metasternum, abdomen coarsely punctate (Fig. 35); female with moderately deep lateral pit on abdominal sternum IV, male pit shallow; male with very small ventral tooth on anterior femur; female without profemoral tooth; hind calcar very small, triangular, pointed (Fig. 36).

Variation.—Material is not sufficient for complete analysis, but it appears that north Queensland specimens differ from more southern ones in having a shallower groove between the parafrontal boss and the temporal lobe, and a broader attachment between the lobe and the boss.

Distribution.—This, the most widely distributed Australian rhysodine, occurs in both tropical and temperate forests, from the vicinity of Cairns in northern Queensland south to Leongatha, Victoria, and, if the holotype label is to be believed, also in Tasmania. It has not been found on the Cape York Peninsula (Fig. 74, Map D).

Localities.—NSW: Lorien Wildlife Refuge, Lansdowne via Taree, 6–11 Jan. 1987, malaise trap (ANIC); Richmond River, no date or collector (ANIC). VIC: Leongatha, 28-11-59 (BPM). QLD: Tinaroo Lk. nr. Kairi, 700 m, 8-XI-1962 (CAS); Malanda, XI-6/7-50 (MCZ); Ravensbourne, 26 mi. N/Toowoomba, 20-VI-1975 (BSRI); Black Mt. Rd., Kuranda, Jan. 2, 1970 (BSRI); Davies ck., Nov. 2, 1969 (BSRI); 29 km S/Mareeba, c.1100 m, 14/15 Dec. 1982 (ANIC); Mt. Finnigan via Helenvale, 760 m, Jul. 20–27, 1974 (QM); Bellenden Ker Rge. 1 km s/Cable Tower 6, Oct. 17–Nov. 5, 1981, 500 m (QM); Herberton Rge., 7–10 km NW/Herberton, 17/18 Dec. 1982 (ANIC); Ravenshoe, 5-3-39 (ANIC); Mt. Spec, 2/71 (ANIC); Ringrose Nat. Prk. via Atherton, 9-xii-1966 (QM); Crater Nat. Prk. via Ravenshoe, 8 Aug. 1968 (QM); Tingaburra, 20-VIII-1966 (QM); 7 km NW/Paluma, 31-14-II-1989, malaise trap (QPIM).

***Kaveinga* (*Angekiva*) *walfordi*, new species**

Type specimens.—Holotype male, labelled "QLD, 29 km. SE of Mareeba, c. 1100 m., 14/15/ Dec. 1982, J.T. Doyen" (ANIC). Paratypes: one female labelled "Mount Spurgeon, N.Q., July 1932, 3500–4000 ft. Australian Harvard Exped., coll. Darlington" (MCZ); one male, labelled "N.E. Qld, Mt. Lewis summit via Julatten, 10 Sept. 1981, G. Monteith, D. Cook, 1200 m., rainforest, log debris, Q.M. Berlesate No. 287 "(QM); one female, labelled "Bellenden Ker Range, N.Q., summit TV sta., 1560 m., 17 Oct.–Nov. 5, 1981, Earthwatch/Qld. Museum" (QM).

Etymology.—Barry Moore first recognized this species as new. We are happy to follow his original intention to name it for Allan Walford-Huggins, a naturalist and collector from Yeppoon, Queensland and to acknowledge the generous help Mr. Walford-Huggins gave us on our recent collecting trip through his area.

Diagnosis.—Distinguished by the absence of a pronotal marginal groove and absence of temporal and angular setae of pronotum; long, narrow median head lobe separating temporal lobes.

Description.—Length 5.1–5.6 mm, antennal segment XI obtuse at tip, without stylet; rings of minor setae and basal setae on segments VI–X (in Mt. Spurgeon specimen, minor setae slightly irregular on segments IX–X); two labral setae; median lobe of head relatively narrow, narrowest opposite middle of eye, tip dilated, spatulate; parafrontal bosses narrow, oblique, depressed; orbital grooves absent; temporal setae absent (Fig. 27); eye relatively small, round (Fig. 29); mentum with one pair of major setae (Fig. 28).

Pronotum relatively long, narrow, L/GW 1.06; lateral margins strongly curved; base only slightly wider than apex; margin shallowly sinuate at hind angle; median groove dilated both anteriorly and posteriorly, constricted at middle; paramedian grooves curved, complete; marginal groove absent; angular seta absent (Fig. 27); prosternum with precoxal carinae; faint punctures confined to margins of precoxal carinae, postpleural sulcus (Fig. 30).

Elytron with one seta in apex of stria IV, about six setae in apical part of stria VII; mestasternum with sides coarsely punctate, disc impunctate or nearly so; coarse punctures on abdominal sterna in one transverse row on sterna III, IV, irregular on sterna V, VI; setae on sternum VI apparently absent; female with lateral pits of sternum IV very shallow (Fig. 31); male pits obsolete.

Male without a ventral tooth on anterior femur but with an indistinct angle in its place; female with anterior femur unmodified; male with very small, narrow hind calcar, latter truncate at tip (Fig. 32); middle tibia without calcar.

Distribution.—A small area in northern Queensland, near Mareeba (Fig. 74, Map B).

Subgenus *Kaveinga* Bell and Bell, 1979

Description.—Antennal stylet absent; antennal segment I pollinose dorsally; ring of minor setae present on segments VI–X; parafrontal boss either distinct or fused to median lobe; 1–3 temporal setae; paramedian grooves of pronotum broad, deep, entirely pollinose, open both anteriorly and posteriorly; marginal groove complete; angular seta present or absent; 0–3 marginal setae; prosternum, propleuron impunctate; precoxal setae absent; elytral setae and pollinosity variously developed; sternum IV of female without enlarged lateral pits; anterior femur without ventral tooth in either sex; femora in most species with dorsal and ventral pollinose strips; middle tibia with row of closely-spaced lateral setae, pits of setae forming serrulate margin in anterior or posterior aspect.

Distribution.—Centered in New Guinea, where there are many species, extending eastward to the Solomon and Santa Cruz islands and the Bismark Archipelago, and west to Celebes and Mindanao. There are about 16 species, of which one occurs in northern Queensland.

Kaveinga (*Kaveinga*) *abbreviata* (Lea)

Rhysodes abbreviatus Lea, 1904:79.

Type specimens.—Syntypes, two, sex unrecorded, labelled "Cairns" (SAMA).

Kaveinga abbreviata: Bell and Bell, 1978:59.
Kaveinga (*sensu stricto*) *abbreviata*: Bell and Bell, 1979:400.

Diagnosis.—The only member of the subgenus in Australia, distinguished by the wide, pilose paramedian grooves, inner carinae abbreviated anteriorly by pollinosity; transverse grooves of ventral abdomen in one continuous pilose punctured row.

Description.—(a more complete description is in Bell and Bell, 1979:400–401). Length 5.2–6.7 mm, parafrontal bosses widely separated from median lobe; orbital groove attaining level of posterior margin of eye.

Pronotum short, broad, L/GW 1.10, widest near middle; paramedian grooves deep, pollinose; width at middle more than half width of outer carina; glabrous areas of carinae strongly abbreviated anteriorly; marginal grooves broad; angular seta present (Fig. 38).

Elytron broad, slightly flattened, humeral tubercle slightly exserted; striae deep, pollinose; intervals narrow, convex; base of elytron with setiferous tubercle opposite stria II (Fig. 41); outer striae subcarinate; stria II with one basal, one apical seta; stria IV with six setae along its length; several setae in apex of stria VII; abdominal sterna III–VI each with an entire transverse, pollinose sulcus (Fig. 39); hind tibia of male with truncate calcar (Fig. 40); male genitalia figured in Bell and Bell (1978:57, Fig. 26).

Distribution.—Northern Queensland from vicinity of Daintree to Millaa Millaa and Babinda (Fig. 74, Map B).

Localities.—QLD: Cairns, 1952 (CAS), same locality (ANIC, MVIC, QM); Upper Little Mulgrave River, SW/Cairns, several dates, VII–VIII 1969 (CAS); Little Mulgrave River (SAMA); Upper Mulgrave R. via Gordonvale, 26/27-xii-1967 (QUIC); Danbulla St. For., 13 km NE/Yungaburra, 21-12/86–13 Jan. 87, intercept trap (QPIM); Tully Falls St. For., 18 km SSW/Ravenshoe, 7-12/87–7/1/88, 730 m, intercept trap (QPIM); Shipton's Flat, 17–19 Oct. 1980 (ANIC); Millaa Millaa (ANIC); 9 mi. N/Daintree, 2/9/69 (ANIC); Gap Creek, 5 mi. N/Bloomfield R., 1001 m (QUIC); Graham Range via Babinda, 9–10 Apr. 1979 (QM); Atherton, Dec. 1962 (MVIC); Kuranda, 19-1-50 (MVIC).

Subtribe Clinidiina

Type genus.—*Clinidium* Kirby, 1835 (Holarctic and Neotropical).

Description.—Minor setae confined to ventral side of antennal segments, forming a narrow crescent-shaped, oval or circular tuft or entirely absent; antennal stylet present; median head lobe short, not extended to neck; frontal grooves complete or nearly so; elytron without apical striole.

Distribution.—Almost cosmopolitan, but absent from Africa (although represented by an endemic genus in Madagascar).

Genus *Rhyzodiastes* Fairmaire, 1895

Type species.—*Rhyzodiastes parumcostatus* Fairmaire, 1895 (Brazil).

Description.—Eyes reduced and modified, hind wings vestigial, paramedian grooves of pronotum complete, elytron with 4–6 striae.

Distribution.—South America, southeast Asia, New Guinea, Australia, New Zealand, Fiji and intervening islands.

There are five subgenera, of which two are found in Australia.

Key to Adults of Australian Subgenera of Rhyzodiastes

1. Paramedian grooves closer together at middle than at base or apex; outer carina much wider at middle than at either end; tufts of minor setae on antennal segments VI–X or VII–X .... *Rhyzoarca* Bell and Bell
1′. Paramedian grooves closer together at ends; outer carina not widened at middle; tufts of minor setae (Australian species) on segments V–X .... *Temoana* Bell and Bell

Subgenus *Rhyzoarca* Bell and Bell, 1985

Type species.—*Rhyzoarca montrouzieri* Chevrolat, 1875 (New Caledonia).

Description.—Tufts of minor setae present on antennal segments VI–X or VII–X, clypeal setae absent, eyes narrowly crescentic, pronotum with outer carinae expanded at middle, so that paramedian grooves are expanded into anterior and posterior pits, narrowed and more or less incurved between pits, pronotal setae absent, marginal and submarginal grooves of pronotum absent, male anterior femur either dentate or tuberculate ventrally (see Bell and Bell, 1985, for full description).

Distribution.—Southeastern Australia, New Zealand, New Caledonia. Two Australian species known.

Key to Adults of Species of Subgenus Rhyzoarca

1. Side of pronotum sinuate anterior to hind angle, latter obtusely denticulate; metasternum with median sulcus .... *Rhyzodiastes* (*Rhyzoarca*) *burnsi* (Oke)

1′. Side of pronotum not sinuate anterior to hind angle, latter rounded; metasternum without medican sulcus .... *Rhyzodiastes* (*Rhyzoarca*) *ovicollis,* new species

Rhyzodiastes (*Rhyzoarca*) *burnsi* (Oke)

Rhysodes burnsi Oke, 1932:148.

Type specimen.—(Sex not recorded) labelled "Mt. Wilson, N.S.W." (MVIC).

Rhyzodiastes burnsi: Bell and Bell, 1978:61.
Rhyzodiastes (*Rhysoarca*) *burnsi*: Bell and Bell, 1985:9.

Diagnosis.—Distinguished by sinuate hind angle of pronotum, metasternum with median sulcus, absence of pronotal marginal groove, tufts of minor setae on antennal segments VI–X.

Description.—Length 6.5–7.0 mm; antennal tufts on segments VI–X; median head lobe moderately long, ending opposite eye; temporal lobes rounded posteriorly; pronotum moderately elongate, L/GW 1.14; front angles obtuse; lateral margin sinuate anterior to hind angle, latter obtusely denticulate; base of pronotum relatively broad, median groove distinctly impressed (Fig. 42).

Elytron with three striae; sutural and parasutural striae coarsely punctate; parasutural stria forms medially-directed scarp near apex; intratubercular stria abbreviated posteriorly; elytral setae absent (Fig. 43); metasternum with median sulcus; abdominal sterna transversely sulcate, interrupted at midline, each sulcus with medial and lateral pit; sternum VI with divided transverse basal sulcus, connected laterally to submarginal sulcus, latter pollinose laterally but becoming row of coarse punctures medially, no punctures anteriorly to submarginal sulcus; sternum VI with two or four setae (Fig. 44).

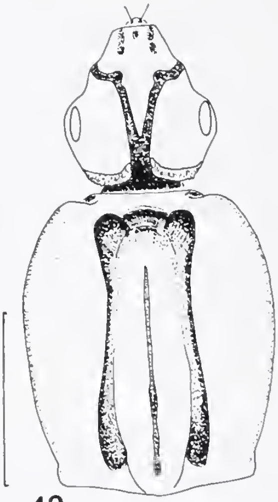
Male anterior trochanter with ventral tooth; male anterior femur with ventral carina with about eight tubercles (Fig. 45); hind trochanter of male rounded; middle calcar curved, cultrate, raised above level of spurs; hind calcar triangular, acute, shorter than middle one, not notched proximally (Fig. 46). Ventral surface of female not studied (for full description, see Bell and Bell, 1985:9).

Distribution.—Known from Mount Wilson, NSW, inland from Sydney, and from Myrtle Mountain, near Eden, suggesting a range in the coastal mountains from the Sydney area nearly to the Victoria border (Fig. 74, Map D).

Localities.—NSW: Mt. Wilson (type locality); 2 males from Myrtle Mt., 8 km N/Wyndham, in log, Aug. 1979 (ANIC).

Variation.—We refer an additional specimen from far northern NSW with doubt to this species. It is a male labelled "Dawsons Spring, Mt. Kaputar, NE. NSW, 30.16.30 S, 150.09.30 E, 1300 m., 18 Nov. 1983, ABRS, AM/QM.RF" (QM). The locality is in the Nandewar Range, east of Narribri, NSW. In most respects it resembles the specimens described above, but differs in the following particulars: length 7.8 mm, pronotum relatively broader, L/GW 1.25; antennal stylet more elongate, chisel-like, truncate; elytron with a conspicuous patch of pollinosity just posterior to the humerus; hind trochanter of male pointed (rather than round); tubercles on ventral side of male anterior femur perhaps more prominent; middle calcar elongate, longer than hind one, not raised above level of spurs, bounded proximally by minute notch; hind calcar more bluntly pointed.

This specimen may be an atypical example of *R. burnsi.* In view of the number



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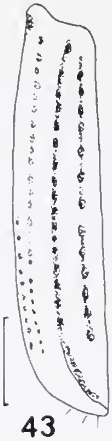

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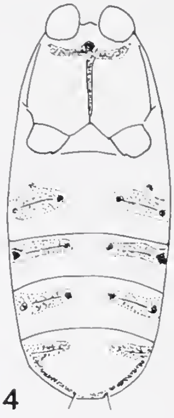

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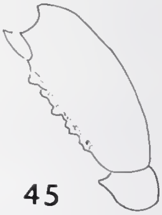

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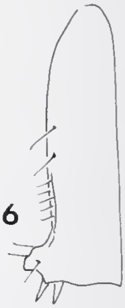

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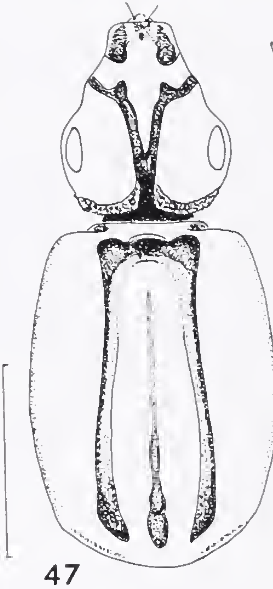

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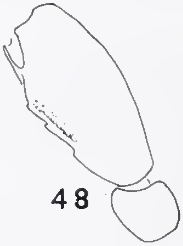

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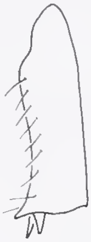

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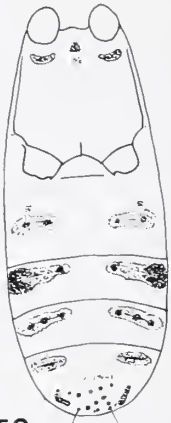

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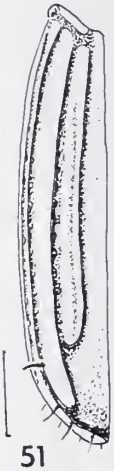

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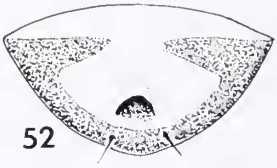

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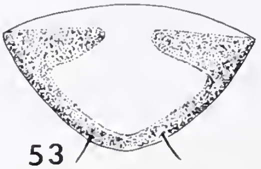

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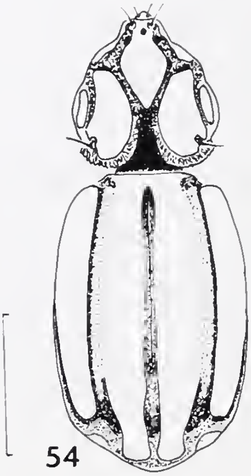

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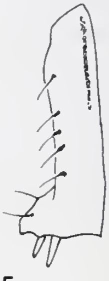

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of small differences and the fact that Mount Kaputar is a very isolated locality, it seems possible that it may represent a distinct taxon. Naming it must await capture of an adequate series of specimens.

Rhyzodiastes* (*Rhyzoarca*) *ovicollis, new species

Type specimen.—Holotype male, labelled "Ramsay's Scrub, Cooloola, S. QLD, Dec. 1975, M. Hockings, pitfall trap, rain forest" (QUIC).

Etymology.—This species is named for the oval shape of the pronotum.

Diagnosis.—Distinguished by more oval shape of pronotum; absence of metasternal median sulcus; absence of pronotal marginal groove; tufts of minor setae on antennal segments VII–X.

Description.—Length 6.7 mm; antennal tufts on segments VII–X; median head lobe relatively long, narrow, ending opposite posterior margin of eye; temporal lobes rounded posteriorly; pronotum elongate, L/GW 1.43, oval, front and hind angles both rounded; hind angle not distinct, margin not sinuate; median groove lightly impressed; posterior median pit distinct (Fig. 47).

Elytron with parasutural striae, impressed and with coarse punctures; intratubercular stria finely punctured, abbreviated posteriorly; marginal stria represented by row of fine punctures in posterior portion; elytral setae absent; metasternum without median sulcus; abdominal sterna with transverse sulci broadly interrupted at midline, each sulcus with three pits; sternum VI with widely divided transverse sulcus at base, submarginal sulcus indistinct, represented near midline by irregular row of coarse punctures; disc of sternum VI with scattered punctures anterior to submarginal sulcus; sternum VI with two setae (Fig. 50).

Male anterior and posterior trochanters rounded, without tooth, male anterior femur with slight carina with suggestion of minute points formed by notches (Fig. 48); middle tibia with small, acute calcar, slightly turned up at tip, not raised above level of spurs, latter unusually small; calcar of hind tibia similar to that of middle tibia, but shorter, less upturned (Fig. 49). Female unknown.

Distribution.—Known only from the type locality, near the Queensland coast, east of Gympie (Fig. 74, Map C).

Subgenus *Temoana* Bell and Bell, 1985

Type species.—*Clinidium spissicorne* Fairmaire, 1985 (Malaya).

Description.—Apical stylet of antenna present; tufts of minor setae on antennal segments IV–X or V–X; clypeal setae present; compound eye narrow, crescentic; genae glabrous ventrad to eye; inner carinae of pronotum sloped gradually to paramedian groove; paramedian grooves straight or slightly convergent to base and apex; outer carina not greatly broadened in middle; intercalary stria of elytron absent. Twenty-five or more species.

Distribution.—From the Caroline and Solomon islands, westward to the Andaman Islands, extreme eastern India and Formosa, south into northern Queensland but absent from New Zealand, New Caledonia, and Fiji. One species known from Australia.

Rhyzodiastes (*Temoana*) *mirabilis* (Lea)

Rhysodes mirabilis Lea, 1904:80.

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Fig. 42–46.—*Rhyzodiastes* (*Rhyzoarca*) *burnsi* (Oke): Fig. 42. Head, pronotum, dorsal aspect; Fig. 43. Left elytron, dorsal aspect; Fig. 44. Metasternum, abdomen, ventral aspect, male; Fig. 45. Trochanter and profemur, male; Fig. 46. Hind tibia, male. Fig. 47–50.—*Rhyzodiastes* (*Rhyzoarca*) *ovicollis*, new species: Fig. 47. Head, pronotum, dorsal aspect; Fig. 48. Trochanter and profemur, male; Fig. 49. Hind tibia, male; Fig. 50. Metasternum, abdomen, ventral aspect, female. Fig. 51–55.—*Rhyzodiastes* (*Temoana*) *mirabilis* (Lea): Fig. 51. Left elytron, dorsal aspect; Fig. 52–53. Sternum VI, ventral aspect, female; Fig. 54. Head, pronotum, dorsal aspect; Fig. 55. Hind tibia, male.

Type specimen.—Holotype, labelled "Cairns, Queensland" (MMUS) (not seen).
Rhyzodiastes mirabilis: Bell and Bell, 1978:61.
Rhyzodiastes (*Temoana*) *mirabilis*: Bell and Bell, 1985:30.

Diagnosis.—Distinguished by the wide inner carina which slopes gradually into the paramedian groove, the presence of tufts of minor setae on antennal segments V–X.

Description.—Length 5.0–8.0 mm; antennal stylet short, somewhat compressed; tufts of minor setae on antennal segments V–X; basal setae of antenna absent; temporal lobes rounded medially, closest together just posterior to tip of median lobe; one temporal seta (Fig. 54).

Pronotum elongate, L/GW 1.56, widest at middle with sides curved; apex less narrowed than base; median groove narrow, deep; inner carinae together forming convex surface; outer carinae broad, 0.5 as wide as inner carinae, not narrowed anteriorly; pronotal setae absent; marginal groove complete, visible in lateral but not dorsal view (Fig. 54).

Elytron with sutural stria impressed, straight; parasutural stria entire; intratubercular stria entire, pollinose; marginal stria narrow, pollinose; setae absent from sutural, parasutural, intratubercular striae; subapical tubercle with 5–6 setae; marginal stria with 5–7 setae near apex (Fig. 51).

Metasternum not sulcate; female with lateral pit of sternum IV large, deep; male with hind trochanter pointed, anterior trochanter toothed; hind calcar triangular (Fig. 55); middle calcar triangular but smaller than hind one; front femur tubercular ventrally.

Distribution.—A limited area in northern Queensland, from 30 km south of Cooktown (Shipton's Flat) to the vicinity of Innisfail (Fig. 74, Map D).

Localities.—QLD: Shipton's Flat (S/Cooktown), June '58 (MCZ); Upper Little Mulgrave R., 3-VIII-69 (CAS); Bellenden Ker (LUN); Redlynch, 12–20, VIII-1938 (BMNH); Kuranda, Jan. 2, 1970 (BSRI); Mt. Lewis Rd., 2M above Bushey Ck., 23-9-66 (ANIC); Daintree, 9/69 (ANIC); Mossman Gorge, 27-X-66 (ANIC); W. slopes of Seymour Rge., Dinner Ck. Rd. nr. Innisfail, at light (ANIC); Babinda, 11/50 (ANIC); Moses Ck., 4 km NE, Mt. Finnigan, 14/16 Oct. 1980 (ANIC); 29 km SE/Mareeba, 100 m, 14/15 Dec. 1982 (ANIC); 30 m Cape Tribulation, Bloomfield Tr., 14 July 1982 (ANIC); 7 mi. SE Yungaburra, 19 Sept. 1972 (BPM); 2 km SE Mt. Spurgeon via Mt. Carbine, 20/21 Dec. 1988, 1100 m (QM); Lamb Range, 19 km SE Mareeba, 11 Dec. 1988, 1100–1200 m (QM); Bloomfield Rd. via Helenvale, July 20–27, 1974 (QM); Graham Range via Babinda, 9/10 Apr. 1979 (QM); Kirrama Range via Kennedy, 700 m, 2/3 Oct. 1980 (QM); Windsor Tableland Rd., 13/1–5/3, 1986, intercept trap (QPIM); Gap. Ck., 5 M. N/Bloomfield River, 8/9-V-1970, 500 ft (QUIC); Cooper Crk., 18 M. N/Daintree River, 20–22-VI-1969 (QUIC); Mt. Edith, 2 mi. N/Tinaroo Dam, 3500 ft 2-VI-1972 (QUIC); Churchill Ck., Mt. Lewis Rd. via Julatten, 27-XI-1969 (QUIC); "The Boulders", Babinda, 15-XII-1966 (QUIC); Noah Ck., S/Cape Tribulation, 13-VIII-71 (UVM); Davies Ck. St. For., Mareeba, 20 Jan 1970 (UVM).

Variation.—Some females have a deep median pit in sternum VI while others lack it (Fig. 52, 53). We can discern no geographic pattern in this variation and we did not see two corresponding types of males. We conclude tentatively that this is polymorphism. Similar variation is known in *Rhyzodiastes* (*Rhyzostrix*) *davidsoni* Bell and Bell of Brazil and *Clinidium* (*Arctoclinidium*) *veneficum* Lewis of Japan.

Subtribe Omoglymmiina

Type genus.—*Omoglymmius* Ganglbauer, 1892.

Description.—Minor setae of antenna forming subapical ring on each outer segment; median lobe of head short, not extended to neck or separating temporal lobes; latter with distinct medial angle in most species; elytral striation complete (seven striae); apical striole distinct in most species.

Distribution.—Almost cosmopolitan, but absent from Madagascar and New Zealand, and poorly represented in Australia, Africa and South America. Only one genus in Australia.

Genus *Omoglymmius* Ganglbauer, 1892

Type species.—Rhysodes germari Ganglbauer, 1892.

Description.—Pronotum without angular seta; paramedian grooves, deep, complete; middle, hind tibiae each with single spur.

Distribution.—As given for subtribe. Two of eleven subgenera occur in Australia.

Key to Adults of Australian Subgenera of Omoglymmiina

1. Antennal segment XI with apical stylet; eye small, less than 0.3 of depth of head; medial margin of subapical tubercle aligned with stria II .... *Caeconavitia* Bell and Bell

1′. Antennal segment XI without apical stylet; eyes large, more than 0.5 of depth of head; medial margin of subapical tubercle aligned with stria IV .... *Omoglymmius*

Subgenus *Caeconavitia* Bell and Bell, 1982

Type species.—Omoglymmius (*Nitiglymmius*) *zimmermani* Bell and Bell, 1978.

Description.—Antennal stylet present; basal setae of antenna absent; clypeal setae absent; eye small, about 0.3 depth of head; medial angles of temporal lobes without translucent areas; postorbital tubercle absent; each gular groove with enlarged pit; marginal groove of pronotum entire; elytral striae impressed; punctures of abdominal sterna in single transverse row on each sternum; medial margin of subapical tubercle aligned with apex of stria II.

The discovery of an Australian member of this subgenus is a considerable surprise, as the only previously known member of the subgenus is found in Fiji. The two species may be separated by the following couplet:

1. Frontal grooves linear, very narrow; frontal space very small; temporal lobe sinuate opposite median pit and also posteriorly, so medial, posterior angles both well defined; male with hind calcar very small obtuse; male with lateral pit on sternum IV .... *Omoglymmius* (*Caeconavitia*) *zimmermani* Bell and Bell

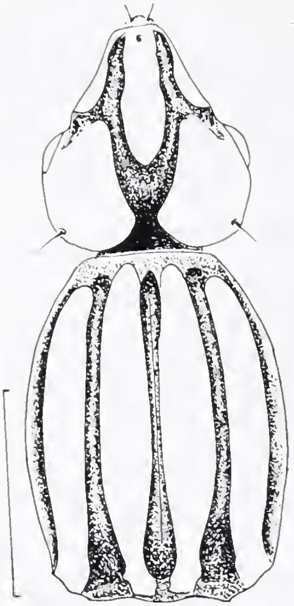
1′. Frontal grooves not linear, wider; frontal space larger, V-shaped; temporal lobes rounded medially; medial, posterior angles not defined; male with hind calcar short, truncate; male without lateral pits on sternum IV ... . *Omoglymmius* (*Caeconavitia*) *okei*, new species

Omoglymmius* (*Caeconavitia*) *okei, new species

Type specimen.—Holotype male, labelled "Blue Mtns., n. QLD, Cape York, 18-5-51, C. Oke" (MVIC). The type locality is at 13.34S-143.13E. The Blue Mountains are an outlier of the McIlwraith Range near the Iron Range (Fig. 74, Map B).

Etymology.—This species is named after Charles Oke, an Australian entomologist, the describer of *Rhyzodiastes burnsi.*

Diagnosis.—Distinguished by the presence of antennal stylet; eye round, reduced; medial margin of subapical tubercle aligned with apex of stria II; punctures of abdominal sterna few in number, arranged in one transverse row across sternum; elongate pronotum; carinae impunctate.



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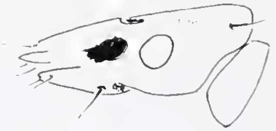

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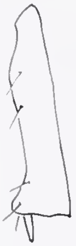

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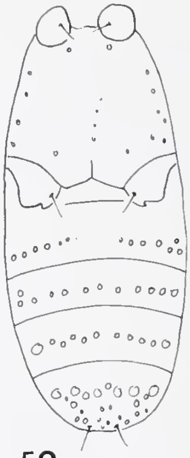

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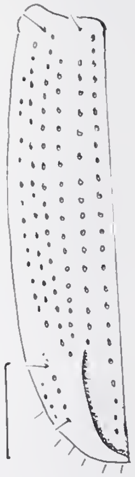

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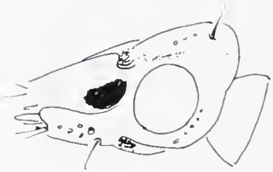

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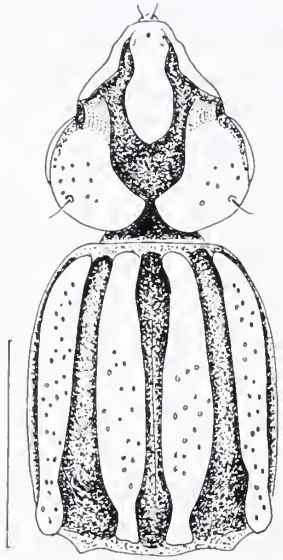

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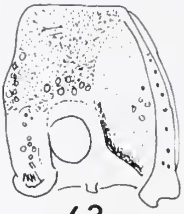

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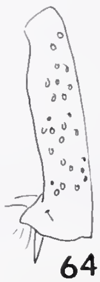

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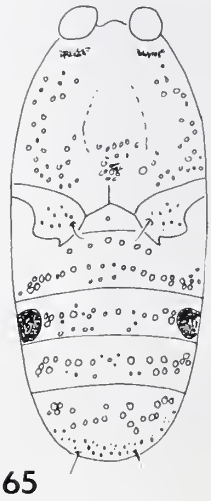

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Description.—Length 6.2 mm; form elongate; ventral surface without opalescence; stylet slender, acute, head with median lobe triangular, apex of latter rounded, opposite middle of eye; frontal grooves moderately wide; orbital groove absent; frontal space V-shaped; medial, posterior angles of temporal lobe rounded; temporal lobe impunctate; one temporal seta (Fig. 56); eye slightly oval, about 0.33 depth of head (Fig. 57); mentum with about eight very coarse punctures; gular grooves dilated posteriorly to form pair of gular pits at base of mentum.

Pronotum relatively long, narrow, L/GW 1.40; margins curved evenly into apex ("collar" absent); inner, outer carinae of nearly even width; all carinae impunctate; median groove deep, posterior part expanded; both sides of paramedian grooves deep, abrupt; lateral margin of pronotum distinctly sinuate anterior to hind angles (Fig. 56); epipleuron with a few indistinct punctures; prosternum with intercoxal pit deep, dilated posteriorly.

Elytron moderately elongate, sides curved; greatest width posterior to middle; humeral tubercles prominent; striae punctate, scarcely impressed; subapical impression deep, limited to first, second intervals; striae III, IV, V ending anterior to subapical impression (Fig. 60); apical striole distinct; stria VI obsolete; two setae in apical striole, about five in apex of stria VII; metasternum with a few coarse punctures along anterior, lateral margins and in midline; sternum IV of male without lateral pits (Fig. 59); profemur of male not dentate; ventrally hind calcar small but well defined, truncate (Fig. 58); female unknown.

Subgenus *Omoglymmius* Ganglbauer, 1892

Description.—Antennal segment XI without a stylet; basal setae of antennal segments absent; clypeal setae absent; frontal grooves deep; temporal setae 0–4; eye deeper than long, in most species fully developed; marginal groove of pronotum complete; spur of middle tibia with tip curved anteriorly; lateral pits present on sternum IV in female, usually suggested in male; hind wing fully developed in most species.

Distribution.—Centered in New Guinea, which has many species, extending to the Caroline Islands in the east and to Europe in the west. Only three species are known from Australia. Each is restricted to northern Queensland, and each is closely related to a species in New Guinea.

Key to Adults of Australian Species of Omoglymmius sensu stricto

1. Postorbital tubercle present, visible in dorsal view .... *Omoglymmius* (*Omoglymmius*) *monteithi* new species
1′. Postorbital tubercle absent 2
2.(1′.) Posterior margin of temporal lobe evenly curved; eye barely visible in dorsal view (although large, evident in lateral view); one temporal seta .... *Omoglymmius* (*Omoglymmius*) *ichthyocephalus* (Lea, 1904)
2′. Posterior margin of temporal lobe bisinuate, forming two projecting lobes in addition to medial angles; eyes relatively prominent, plainly visible in dorsal view; 2–4 temporal setae .... *Omoglymmius* (*Omoglymmius*) *bituberculatus* new species

Omoglymmius* (*Omoglymmius*) *ichthyocephalus (Lea), new combination

Rhysodes ichthyocephalus Lea, 1904:79.

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Fig. 56–60.—*Omoglymmius* (*Caeconavitia*) *okei*, new species: Fig. 56. Head, pronotum, dorsal aspect; Fig. 57. Head, left lateral aspect; Fig. 58. Hind tibia, male; Fig. 59. Metasternum, abdomen, ventral aspect, male; Fig. 60. Left elytron, dorsal aspect. Fig. 61–65.—*Omoglymmius* (*Omoglymmius*) *ichthyocephalus* (Lea): Fig. 61. Head, pronotum, dorsal aspect; Fig. 62. Head, left lateral aspect; Fig. 63. Prothorax, left ventrolateral aspect; Fig. 64. Hind tibia, male; Fig. 65. Metasternum, abdomen, ventral aspect, female.

Type specimen.—Holotype (presumed) from Cairns, Queensland, sex not recorded (SAMA).

Omoglymmius ichthyocephalus: Moore, 1987:22.

Diagnosis.—Distinguished by absence of postorbital tubercle; temporal lobe reniform, medial margin curved; outer carinae slightly narrower than inner carinae, parallel sided; one temporal seta.

Description.—Length 6.0–7.6 mm; antennal segments I–IV coarsely punctate, V–X more sparsely, finely so; XI impunctate; head longer than wide; median lobe short, oval, impunctate, its tip rounded; frontal space slightly broader than long, margins shallowly curved; medial angles obtuse, slightly separated; posterolateral margin nearly evenly rounded; occipital angle rounded, scarcely evident; orbital groove narrow, traceable about to middle of eye; anterior portion of temporal lobe a convex, pollinose ridge, glabrous part of temporal lobe thus widely separated from antennal lobe; temporal lobe with about 12 punctures; one temporal seta (Fig. 61); postorbital, suborbital tubercles absent (Fig. 62); eye large, round, but flat, scarcely visible in dorsal view.

Pronotum rather short, subquadrate, L/GW 1.13; base slightly narrowed, apex more distinctly narrower, lateral margins slightly curved, margins not sinuate anterior to hind angle; outer carina about 0.67 as wide as inner carina at middle; medial margin of outer carina scarcely sinuate; outer carina widest at middle, narrowed at apex; inner carina narrowed nearly to base, but dilated at extreme base; outer carina with about 35 fine punctures, inner carina with 10–15 fine punctures; pronotum without setae (Fig. 61); prosternum extensively pollinose anteriorly, without precoxal carinae (Fig. 63).

Elytron relatively long, narrow; striae impressed, coarsely punctate; transverse basal scarp pollinose; base of stria IV with very short, longitudinal pollinose scarp; stria IV with one seta near apex; apical striole with one seta; stria VII with several setae near apex; metasternum entirely, coarsely punctate; abdominal sterna III–V coarsely punctate, punctures becoming coarser, confluent laterally; posterior punctures of each sternum notably finer than anterior ones; lateral pit present on sternum IV in both sexes (Fig. 65); male with ventral tooth on profemur; middle calcar obtuse, slightly concave dorsally; hind calcar obtuse, triangular, with several setae (Fig. 64).

Remarks.—This species is most closely related to *Omoglymmius oroensis* Bell and Bell of New Guinea, and would key to that species in the general key of Bell and Bell (1982:180–187). In *O. oroensis,* the median lobe has a few punctures; the temporal lobes are less rounded, the medial angles are more separated; the orbital groove is better developed; the pronotum is more narrowed anteriorly; the outer carina is less narrowed at its base; both carinae have fewer punctures and the calcars differ in shape.

Distribution.—Northern Queensland from Cape York, south to Cairns (Fig. 74, Map C).

Localities.—QLD: 11 km ENE/Mt. Tozer, 11–16, July 1986 (ANIC); Somerset (SAMA, ANIC, MVIC); Iron Range, Cape York pen., 1–9 June 1971, 5–10 May 1988 (QUIC); Locherbie, Cape York, 6–10-VI-1969 (QUIC).

***Omoglymmius* (*Omoglymmius*) *bituberculatus*, new species**

Type specimens.—Holotype male, labelled "Boar Pkt., N.Q., 12/69, J.G. Brooks, M.470" (ANIC). Paratypes: one female, labelled "Cleveland Bay", (ANIC), (on permanent loan from MMUS); two females, labelled "2 km. N by E, Mt. Tiptree, 17.03S-144.37E, 1 Apr. 1984, A. Calder, T. Weir" (ANIC); one male, labelled "Tribulation Area, 16.03S to 16.05S, 145.28E, 21–28 Mar 1984, A. Calder & T. Weir" (ANIC); one male, labelled "Queensland" (MNHN).

Etymology.—The name of this species is based on the presence of two small tubercules on the posterior margin of the temporal lobes.

Diagnosis.—Distingiushed by absence of postorbital tubercles; posterior margins of temporal lobes bisinuate to form two projecting lobes; 3–5 temporal setae.

Description.—Length 5.8–7.1 mm; antennal segment I coarsely punctate, somewhat pollinose; segments II–X faintly punctate; segment XI impunctate; head longer than wide; median lobe moderately long, shield-shaped, obtusely angled to rounded at apex, impunctate; frontal space longer than broad, U-shaped; margins strongly curved; medial angles well defined; posterior margin bisinuate, defining two projecting lobes; orbital groove short, ill-defined; anterior portion of temporal lobe glabrous, separated from antennal lobe by narrow groove; temporal lobe with 20–30 punctures; temporal setae 3–4 (Fig. 66); postorbital, suborbital tubercles absent (marginal tubercles mentioned above are dorsad to eye); eye large, round, more protruding than in other members of subgenus (Fig. 67).

Pronotum slightly longer than wide; L/GW 1.17; margins curved, base moderately narrowed, apex more strongly so; margin not sinuate anterior to hind angles; outer carina slightly wider than inner one at middle; outer carina widest at middle, tapering to sharp angle anteriorly, truncate posteriorly; inner carina narrowed near base but dilated at extreme base; outer carina with about 38–47 moderately coarse punctures; inner carina with 1–10 very fine punctures; pronotal setae absent (Fig. 66); prosternum punctate, anterior margins pollinose; precoxal carina absent.

Elytron moderately elongate, striae shallow, finely punctate; lateral striae more coarsely punctate than medial ones; outer intervals convex; basal transverse scarp glabrous; base of stria IV with shallow longitudinal pollinose scarp; stria IV with one seta at apex; apical striole without setae; stria VII with several setae near apex; metasternum entirely finely punctate; abdominal sterna III–V entirely finely punctate; both sexes with deep lateral pit on sternum IV (Fig. 68); male with small ventral tooth on profemur, female without such tooth; middle calcar of male acute, small; hind calcar large, tip obtuse, lobate (Fig. 69).

Remarks.—This species is related to *O. aristeus* Bell and Bell of New Guinea, which also has more than one temporal seta but has the temporal lobe evenly rounded.

Distribution.—Northern Queensland from Cairns to Townsville and possibly Dorrigo, NSW (Fig. 74, Map C) (see Variation).

Localities.—QLD: Davies ck. via Mareeba, 8-10-1989 (QPIM); Tinaroo Ck. Rd., Atherton T'land, 15-XII-1989 (UVM).

Variation.—A female specimen labelled "Dorrigo, NSW, Jan. 1931, C. Oke" (MVIC), listed by Oke as *Rhysodes ichthyocephalus,* agrees with the type series except that it has the marginal tubercles of the temporal lobe much smaller. We refer it to this species with doubt and it may well represent a distinct taxon.

***Omoglymmius* (*Omoglymmius*) *monteithi*, new species**

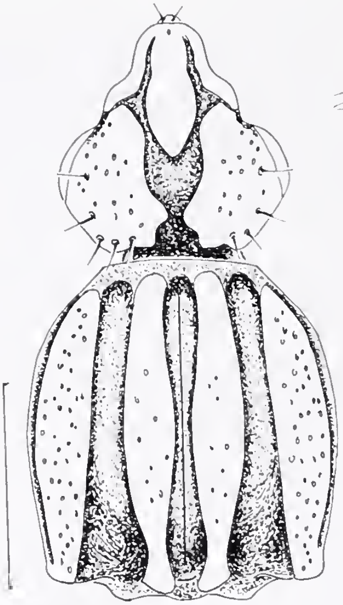
Type specimens.—Holotype female, labelled "West Claudie R., Iron Range, n. Qld, 3–10 Dec. 1985, G. Monteith & D. Cook, rainforest, 50 m" (QM). Paratypes: two females (on same mount), labelled "West Claudie R., Iron Range, n. Qld 29/30-IX-1974, G.B. Monteith, rainforest" (QM); one female, labelled "Cape York Pen., West Claudie R., Iron Range, Oct. 2, 1974, coll. M.S., B.S. Moulds" (UVM).

Etymology.—This species is named for Dr. G. B. Monteith of the Queensland Museum, Brisbane, in gratitude for his help with this project.

Diagnosis.—Distinguished by presence of postorbital tubercle, visible in dorsal view.

Description.—Length 6.8–7.0 mm; antennal segments I–VIII finely punctate; segments IX, X very finely punctate, XI impunctate; head longer than wide; median lobe oval, tip nearly rounded; frontal space wide, U-shaped, its lateral margin curved; medial angles obtuse, narrowly separated; antennal lobe connected to temporal lobe by pilose ridge; orbital groove indistinct, represented by pollinose area extending posterior to middle of eye; temporal lobe with 12–15 fine punctures, area along medial margin impunctate; one temporal seta (Fig. 70); postorbital tubercle visible in dorsal view, pollinose; width across temporal lobes slightly less than that across eyes, eye large, round (Fig. 71).

Pronotum elongate, L/GW 1.22, widest near middle; base slightly narrowed; apex strongly narrowed; lateral margins only slightly curved posteriorly, more strongly so anteriorly; margin scarcely sinuate anterior to hind angle; outer carina slightly narrower than inner one at middle; medial margin of outer



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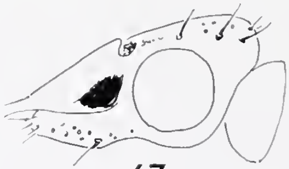

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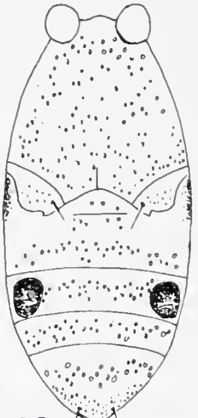

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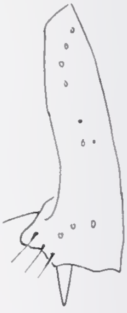

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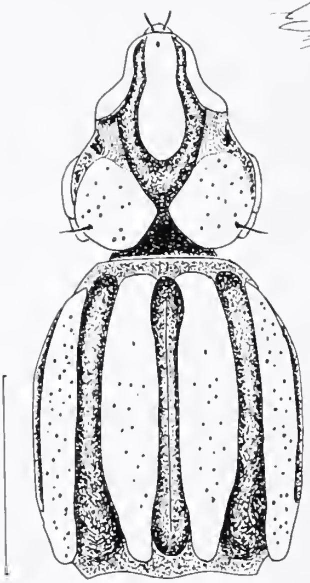

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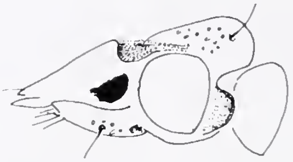

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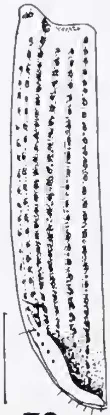

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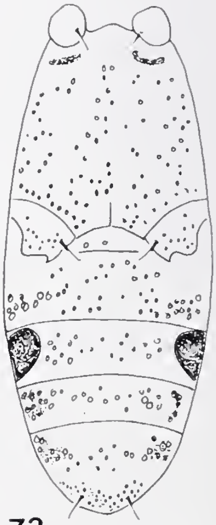

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carina not angled or scarcely angled near base; outer carina slightly narrowed posteriorly, strongly so anteriorly; inner carina narrowly subtruncate at apex; outer carina with 22–26 fine punctures; inner carina with 11–18 fine punctures; pronotum without setae (Fig. 70); prosternum without precoxal carina.

Elytron rather narrow, elongate; striae not impressed, rather coarsely punctate, base of stria IV with short longitudinal pilose scarp; basal transverse scarp pollinose from stria IV to suture; one seta near apex of stria IV, one seta in apical striole; 4–5 setae near apex of marginal stria (Fig. 72); metasternum entirely punctate; abdominal sterna III–V with coarse, scattered punctures partly coalescent laterally on V, VI; female wtih large lateral pits on sternum IV (Fig. 73); male unknown.

Remarks.—The presence of postorbital tubercles easily separates this species from other known Australian *Omoglymmius s. str.* It is most similar to *Omoglymmius sus* Bell and Bell, 1982 among the New Guinean species, which it resembles in having the metasternum entirely punctate and in having a narrow, pollinose ridge connecting the antennal and temporal lobes. However, the postorbital tubercles of *O. sus* are larger, the width across them exceeding the width across the eyes.

Distribution.—Rain forests of the Iron Range on Cape York Peninsula (Fig. 74, Map D).

Variation.—A female specimen labelled "Iron Range, Cape York Pen. n. QLD, June 30–July 4, 1977, G. B. Monteith" (QM) differs from the type series in having two temporal setae. It will probably prove to be a variant of this species.

ZOOGEOGRAPHY

The Rhysodini in Australia are limited to relatively wet types of forest; consequently they are confined to a long, narrow strip along the east coast, extending from Cape York to Tasmania (Fig. 74, Map A). In the tropical zone, they are known only from the true rain forest. In the temperate zone, south of the Tropic of Capricorn, they are found both in temperate rain forest and wet sclerophyll forest. In Tasmania they are probably limited to wet sclerophyll forest. The evidence for this is based solely on two specimens with insufficient locality data, citing them as coming from the Hobart area. We failed to discover any specimens in the Tasmanian rain forest. Darlington (1961) discussed Australian rain forests in detail and in a further publication included additional information on the tropical part of the rain forest (Darlington, 1971). He also used the distribution of Carabidae (not including the Rhysodini), especially the flightless groups, to make inferences about the histories of separate patches of rain forest.

The humid forests are interrupted by many gaps, some very extensive, where the mountain ranges support only dry sclerophyll forest, apparently not suitable for Rhysodini or the more specialized terrestrial forest Carabidae. The tropical rain forests are divided into five widely separated units, mapped by Darlington (1961, 1971). These are the tip-of-peninsula rain forest at Cape York, the midpeninsular rain forest, including the McIlwraith Range, Mount Tozer and the Iron Range, the base-of-peninsula rain forest, extending from just south of Cooktown to just north of Townsville, the Elliot Range rain forest just south of Townsville

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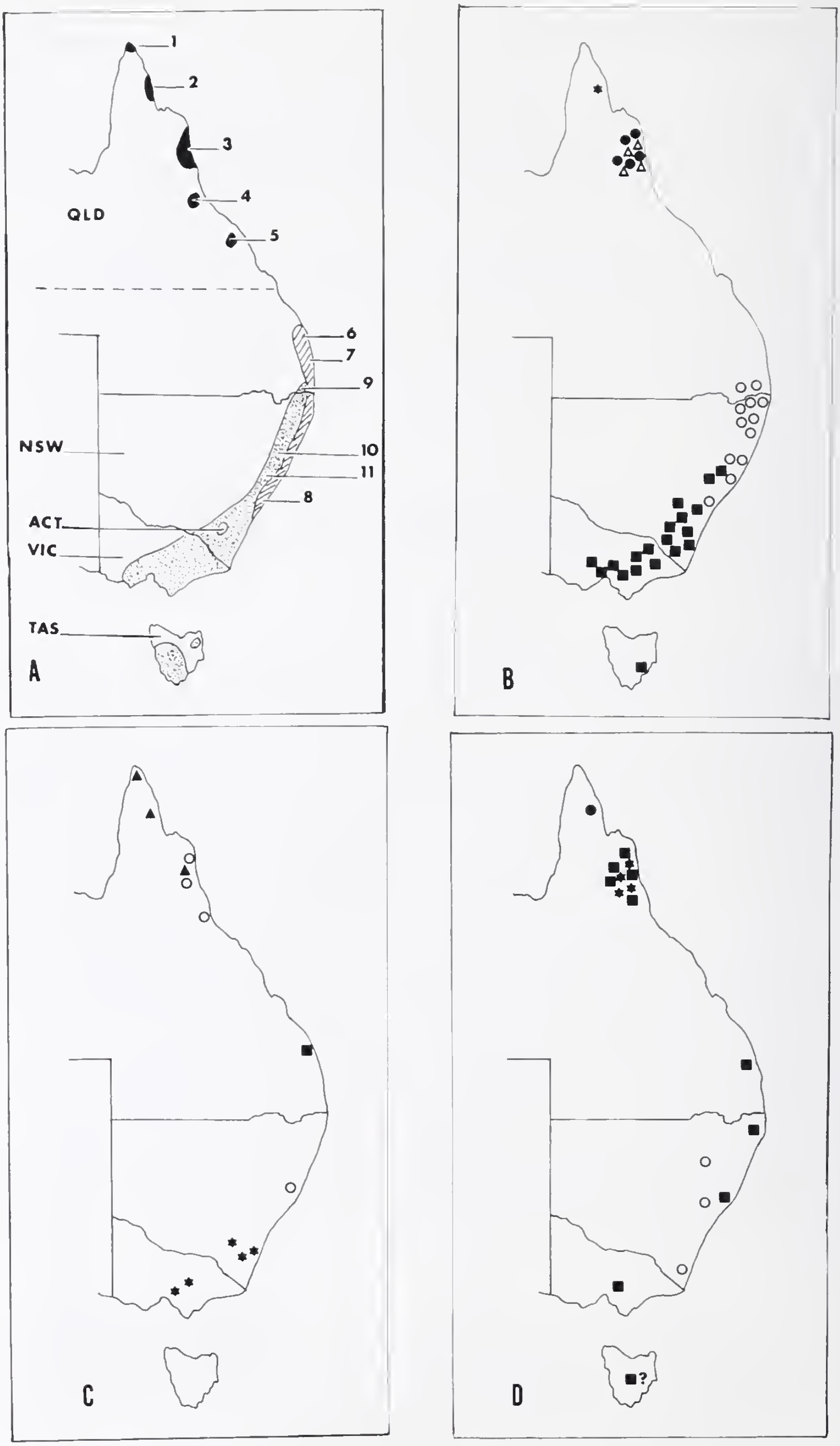
Fig. 66–69.—*Omoglymmius* (*Omoglymmius*) *bituberculatus*, new species: Fig. 66. Head, pronotum, dorsal aspect; Fig. 67. Head, left lateral aspect; Fig. 68. Metasternum, abdomen, ventral aspect, female; Fig. 69. Hind tibia, male. Fig. 70–73.—*Omoglymmius* (*Omoglymmius*) *monteithi*, new species: Fig. 70. Head, prothorax, dorsal aspect; Fig. 71. Head, left lateral aspect; Fig. 72. Left elytron, dorsal aspect; Fig. 73. Metasternum, abdomen, ventral aspect, female.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and the Eungella Range rain forest, inland from Mackay. According to Darlington, the flightless Carabidae support the conclusion that each of these islands of rain forest has been separated sufficiently long to have developed an endemic fauna. The midpeninsular forest has been separated for a very long time from the base-of-peninsula forest. The tip-of-peninsula forest is a relatively small area with an impoverished fauna, suggesting that it evolved *in situ* by accumulation of relatively few immigrants from other areas of rain forest. The winged Carabidae of this area and the midpeninsular forest include many Carabidae shared with New Guinea and others only slightly differentiated from New Guinean relatives, but this element is entirely absent from the flightless Carabidae. Darlington concluded that the Pleistocene land connection between the two land masses did not include continuous rain forest, thus forming a barrier to flightless Carabidae.

Subtropical rain forest occupies the Coastal Plain and nearby mountains in southeastern Queensland and northern and central New South Wales, from about the vicinity of Gympie, Qld. south to Sydney and beyond, becoming more attenuated at the southern end of the range. Enclaves of temperate rain forest occur in the higher mountains as far north as the Mount Lamington area, just north of the Queensland-New South Wales border and in the Dorrigo Plateau, with scattered areas farther south, and more extensive areas in East Gippsland, the most eastern part of Victoria. Cold temperate rain forest occupies most of the southwestern part of Tasmania, in addition to a smaller area in the northeastern sector. The subtropical and temperate rain forests and wet sclerophyll forests are interrupted by areas of drier forest, but these barriers are neither as broad nor apparently as old as those in the tropical rain forest, and show less clear-cut relationships to rhysodine distributions.

Among the rhysodines in Australia, only *Kaveinga* (*Angekiva*) *frontalis* is widely distributed, from the base-of-peninsula rain forest in Queensland, south through subtropical and temperate rain forests to Victoria and probably Tasmania. Of the tropical rain forests, only the base-of-peninsula forest has been adequately collected. Six species are known: *Kaveinga* (*Angekiva*) *stiletto, Kaveinga* (*A.*) *frontalis, Kaveinga* (*Kaveinga*) *abbreviata, Rhyzodiastes* (*Temoana*) *mirabilis, Omoglymmius* (*Omoglymmius*) *ichthyocephalus* and *O.* (*O.*) *bituberculatus.* Three species are known from the midpeninsular rain forest: *Omoglymmius* (*Omoglymmius*) *ichthyocephalus,* shared with the preceding forest and two not found there: *Omoglymmius* (*Caeconavitia*) *okei* and *Omoglymmius* (*Omoglymmius*) *monteithi.* In

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Fig. 74.—Eastern Australia showing distribution of humid forests (adapted from Darlington, 1961) and distribution of species. Map A. Dark shading, tropical rain forests; diagonal lines, subtropical rain forests; dotted areas, general zone of temperate rain forest and wet sclerophyll (forests are discontinuous and zones are generalized). 1. Cape York tip-of-peninsula rain forest. 2. Iron Range, midpeninsular rain forest. 3. Cairns area, base-of-peninsula rain forest. 4. Elliot Range. 5. Eungella Range. 6. Cooloola National Park. 7. Brisbane. 8. Sydney. 9. Lamington National Park. 10. Dorrigo Plateau. 11. Barrington Tops National Park. Horizontal dashed line represents the Tropic of Capricorn. Map B. Black squares, *Leoglymmius lignarius*; open circles, *Kaveinga* (*Angekiva*) *stiletto*; black circles, *Kaveinga* (*Kaveinga*) *abbreviata*; open triangles, *Kaveinga* (*Angekiva*) *walfordi*; star, *Omoglymmius* (*Caeconavitia*) *okei*. Map C. Stars, *Sloanoglymmius planatus*; open circles, *Omoglymmius* (*Omoglymmius*) *bituberculatus*; black triangles, *Omoglymmius* (*Omoglymmius*) *ichthyocephalus*; black square, *Rhyzodiastes* (*Rhyzoarca*) *ovicollis*. Map D. Black squares, *Kaveinga* (*Angekiva*) *frontalis,* question mark denotes unspecific locality; open circles, *Rhyzodiastes* (*Rhyzoarca*) *burnsi*; stars, *Rhyzodiastes* (*Temoana*) *mirabilis*; black circle, *Omoglymmius* (*Omoglymmius*) *monteithi.*

the tip-of-peninsula forest only *Omoglymmius* (*Omoglymmius*) *ichthyocephalus* has been recorded. However, neither the tip nor midpeninsular forests have been adequately collected, as they are remote and difficult of access. No rhysodines have yet been collected in the Elliot or Eungella ranges, although they would be expected there.

In the subtropical forests, three species have been recorded: *Kaveinga* (*Angekiva*) *frontalis, Kaveinga* (*A.*) *stiletto,* and *Rhyzodiastes* (*Rhyzoarca*) *ovicollis.* In the temperate forests, including small patches of wet sclerophyll in otherwise drier mountains, are *Sloanoglymmius planatus* and *Leoglymmius lignarius,* the latter being more widespread and apparently doing better in dry areas. Probably *Kaveinga* (*Angekiva*) *frontalis* should also be included among the temperate species, although known records are near the coast. *Rhyzodiastes* (*Rhyzoarca*) *burnsi* appears to be a warm temperate species on the basis of two known localities.

The Australian rhysodine fauna is still inadequately known and several important questions, both taxonomic and zoogeographic, remain to be answered. For instance, it is not clear whether or not *Rhyzodiastes* (*Rhyzoarca*) *burnsi* and *R.* (*R.*) *ovicollis* are really allopatric, as it appears on the basis of the few known specimens, and whether the one specimen from Mount Kaputar, in northern New South Wales, is *Rhyzodiastes* (*R.*) *burnsi* or another, closely related species. The specimen tentatively attributed to *Omoglymmius* (*Omoglymmius*) *bituberculatus* from the Dorrigo Plateau of New South Wales might prove to be a distinct taxon, or may have an erroneous locality label. Neither of the two records from Tasmania is entirely satisfactory. The type specimen of *Kaveinga* (*Angekiva*) *frontalis* lacks a specific locality, name of collector and date, and might possibly have been collected on the adjacent mainland. The specimen of *Leoglymmius lignarius* was collected in firewood from the Hobart area. The wood was certainly from Tasmania, but the exact source is unknown.

The world distribution of Rhysodini has been discussed previously (Bell, 1979). The present paper does not materially alter the picture, which will be summarized here. The relationship of the Australian rhysodines to those of the rest of the world shows suggestive analogies to the distributions of terrestrial mammals. *Leoglymmius* and *Sloanoglymmius* have plesiomorphic features not found in other rhysodines and are found only in Australia. In both respects they resemble the monotreme mammals (platypus and echidna). Like the latter group, these genera are probably relics of an ancient East Gondwanian fauna (Antarctica and Australia, before the land masses separated). *Rhyzodiastes* (subtribe Clinidiina) is shared with South America, but not with other continents, suggesting a history similar to that of the marsupials (a spread into East Gondwana via a land bridge from South America). *Rhyzodiastes* differs from the marsupials in that it occurs also in New Zealand, New Caledonia and Fiji, extending farther west through the Indonesian islands to Formosa and the Indochina Peninsula. *Omoglymmius* is the only genus in the widespread subtribe Omoglymmiina which reaches Australia. *Omoglymmius* thus corresponds to the muroid rodents among terrestrial placental mammals. Australian representatives of *Omoglymmius* (*Omoglymmius*) are members of a subgenus which ranges from Eurasia to the Caroline Islands. It is represented by a great number of species in New Guinea and undescribed species are still being discovered. The few Australian species appear to be relatively recent immigrants from New Guinea. An older immigrant perhaps is *Omoglymmius* (*Caeconavitia*) *okei* with its only close relative in Fiji.

The most enigmatic subtribe is Rhysodina, with *Kaveinga* widespread in the southwest Pacific from Mindanao and Celebes to Fiji, New Caledonia, New Zealand and Australia, *Kupeus* in New Zealand and *Rhysodes* in the Palearctic, with one species in northern Europe and the other in Siberia and Japan. *Kaveinga* has four subgenera, *Kaveinga* (*Kaveinga*) occurs from the Solomon Islands, New Guinea, and Mindanao to Celebes and is represented by one species in northern Queensland. Subgenus *Angekiva* is endemic to Australia, including Tasmania. Of the two remaining subgenera, one is confined to New Zealand, the other is shared by New Zealand and New Caledonia. The richness of Rhysodina in the southwestern Pacific and their near absence elsewhere suggests an origin in this region with rafting of some species to islands farther west. The presence of *Rhysodes* in the Palearctic Realm is a puzzle. Perhaps, like *Leoglymmius* and *Sloanoglymmius,* the ancestor of the subtribe was a member of an ancient Gondwanian fauna. The ancestor of *Rhysodes* may have rafted westward until it reached the Asian mainland. The absence of any Rhysodina from South America suggests that the subtribe did not come from that continent. Its absence from North America suggests that late arrival in the Palearctic may have prevented access via the Bering land bridge in the Pleistocene. *Rhysodes* is the most cold tolerant of all Rhysodini, being found as far north as southern Sweden and southeastern Siberia, so it otherwise would have been expected to have a good chance to cross the land bridge.

ACKNOWLEDGMENTS

We wish to thank the numerous curators of the following museums in Australia who gave us access to their collections and sent us loans of specimens: Dr. Arturs Neboiss, Museum of Victoria; Dr. E.G. Matthews, South Australian Museum, Adelaide; Dr. Margaret A. Schneider, University of Queensland; Dr. Geoff B. Monteith, Queensland Museum; Dr. Ross I. Storey, Department of Primary Industries, Mareeba; Mr. Peter B. McQuillan, Department of Agriculture, Tasmania; Dr. Alison Green, Tasmania Museum and Mr. Richard Bashford, Forestry Commission, Tasmania. We are especially appreciative of the help Dr. John Lawrence gave us in providing excellent working conditions at the Australian National Insect Collection (CSIRO) in Canberra, and in his valuable assistance collecting specimens in the field and implementing various loans. Our special thanks go to Dr. Barry P. Moore, also at CSIRO, who did some of the original groundwork on the rhysodids of Australia and provided us with access to his collection, assistance on many field trips, advice on unique collecting sites, contacts with other entomologists and help in many other countless ways throughout the year. We are extremely indebted to him. Also at CSIRO, we were given valuable help either in the laboratory or in the field by Dr. Thomas Weir, Dr. Andrew Calder and Mr. Walter Dressler. Michael Hansen, a visiting entomologist from the University of Copenhagen, helpfully contributed to our field work. Dr. Monteith also gave us valuable advice on collecting sites and collectors on our trip to northern Queensland. On our trip to Tasmania, assistance was also given by the private collectors, Dr. George F. Bornemissza, Mr. David Cowie and especially Mr. Michael Bouffard. Mr. Bouffard, a graduate of the University of Vermont now living in Huonville, contributed much of his valuable time and effort in collecting with us in eastern central Tasmania and on Bruny Island. On our trip to Queensland we were given rhysodid specimens by Alan Walford-Huggins and Jack Hasenpusch for which we are greatly appreciative.

Loan material was also sent to us from non-Australian sources. For this material we are very indebted to: Dr. S. Endrödy-Younga (TM); Dr. Nigel Stork (BMNH); Drs. H. and A. Howden (BSRI); Dr. D. Kavanaugh (CAS) and Dr. G. A. Samuelson of the Bishop Museum, Honolulu. We thank Janine Sutphen for the careful typing of the manuscript. We are also indebted to Mr. Brian Macklin for various kinds of help during our stay in Tasmania.

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ANNALS OF CARNEGIE MUSEUM

Vol. 60, Number 3, Pp. 211–241 4 September 1991

A STUDY OF THE VESPIDAE DESCRIBED BY WILLIAM J. FOX (INSECTA: HYMENOPTERA), WITH ASSESSMENT OF TAXONOMIC IMPLICATIONS

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Abstract

The Vespidae described by William J. Fox and deposited in The Carnegie Museum of Natural History are reviewed. Lectotypes are designated for most of the species. New synonymy is as follows: Eumeninae—*Tricomenes* Giordani Soika, 1978 = *Pirhosigma* Giordani Soika, 1978; *Nortonia lugens* Schulthess, 1904 and *Odynerus paraguayensis* Brèthes, 1909 = *Stenonartonia apicipennis* (Fox, 1902). New combinations are: Polistinae—*Agelaia angulata* (Fabricius), *Agelaia angulicollis* (Spinola), *Agelaia fulvofasciata* (DeGeer), *Agelaia multipicta* (Haliday), *Agelaia myrmecophila* (Ducke), *Agelaia pallipes* (Olivier), *Agelaia testacea* (Fabricius), *Protopolybia chartergoides* (Gribodo), *Protopolybia fuscatus* (Fox); Eumeninae—*Ancistroceroides atripes* (Fox), *Ancistroceroides conjunctus* (Fox), *Ancistroceroides cordatus* (Fox), *Ancistroceroides fulvimaculus* (Fox), *Ancistroceroides rufimaculus* (Fox), *Cephalastor rufosuffusus* (Fox), *Hypancistrocerus abdominalis* (Fox), *Hypancistrocerus coxalis* (Fox), *Hypancistrocerus dentiformis* (Fox), *Hypancistrocerus inusitatus* (Fox), *Hypancistrocerus reflectorius* (Dalla Torre), *Pachodynerus corumbae* (Fox), *Pachodynerus sericeus* (Fox), *Parancistrocerus areatus* (Fox), *Parancistrocerus dorsonotatus* (Fox), *Parancistrocerus herbertii* (Fox), *Parancistrocerus longicornutus* (Dalla Torre), *Parancistrocerus striatus* (Fox), *Pirhosigma pilosum* (Fox), *Stenodynerus convolutus* (Fox), *Stenodynerus suffusus* (Fox), and *Stenonartonia apicipennis* (Fox). Changes in status are as follows. Polistinae—*Mischocyttarus picturatus* Bequaert is raised to specific rank; and *Parachartergus smithii* var. *fasciatus* (Fox) = *P. smithii* (Saussure). Eumeninae—*Alphamenes campanulatus gladiator* Giordani Soika, *A. c. luctuosus* Giordani Soika, *A. c. mango,* and *A. c. nanicolor* = *A. campanulatus* (Fabricius); *Eumenes filiformis* Saussure, *E. fulvomaculatus* Fox and *E. rufomaculatus* Fox are treated again as distinct species; *Minixi brasilianum compactum* (Fox) = *M. brasilianum* (Saussure); *Omicron aequale jucundum* Giordani Soika and *O. a. nigritum* Giordani Soika = *O. aequale* Giordani Soika; *Pirhosigma superficiale impurum* Giordani Soika = *superficiale* (Fox); and *Pseudodynerus griseus* (Fox) is raised again to specific rank.

Introduction

Around the beginning of this century the American hymenopterist William J. Fox described a large number of aculeate Hymenoptera from Brazil. His work was based on an extensive collection made by Herbert H. Smith in the period 1874–86. Details on the localities where this material was obtained were given by Fox (1896) in a first contribution dealing with the Scoliidae. The Vespidae were treated in three contributions: Polistinae in no. 5 (Fox, 1898), and Eumeninae in contributions no. 7 (*Zethus, Labus, Eumenes, Montezumia, Monobia*; Fox, 1899) and no. 8 (*Odynerus*; Fox, 1902). The great majority of the specimens described or recorded by Fox are deposited in The Carnegie Museum of Natural History (CMNH). However, syntypes of a number of species were sent by Hugo Kahl in 1937 to Joseph Bequaert, who discussed them in some of his papers, and retained a few specimens in the collection of the Museum of Comparative Zoology

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Submitted 26 June 1990.

(MCZ). Naumann (1968) examined the Carnegie Museum material of *Brachygastra* for his revision, but Richards did not study the collection for his monograph on Neotropical Polistinae (1978). Rather, he examined material retained or determined by Bequaert. Thus, lectotypes were never designated for most of the social wasps. Most of the *Zethus* were studied by Bohart and Stange (1962, 1965), who designated lectotypes. Giordani Soika (1978, 1990) studied syntypes of the *Eumenes,* but for the most part did not designate lectotypes. The remaining material has been unstudied. Although Fox's descriptions are fairly extensive and accurate for that time, it has proven very difficult to identify his species without consulting the type material. Due to the large number of new species he described in *Odynerus,* the "Fox collection" is presently the single most important collection of Neotropical Eumeninae unstudied by modern workers. Research on the Neotropical fauna will be hindered until these species are assigned to genera according to current generic concepts (*cf.* Carpenter, 1986).

This study of the Fox collection began in 1974, when, through the intermediary of Karl V. Krombein, George F. Wallace of The Carnegie Museum of Natural History made the Fox collection of Eumeninae available for detailed study by van der Vecht. Van der Vecht in turn made the species described in the genus *Eumenes* available to A. Giordani Soika for study during one of the latter's visits to The Netherlands. The results of Giordani Soika's work were included in the revision of Neotropical *Eumenes* and related genera (Giordani Soika, 1978, 1990), where he referred to syntypes labelled as lectotypes by van der Vecht. However, no lectotype designations were published by van der Vecht, who was unable to complete the work. He therefore requested that Carpenter, who was studying the cladistic relationships of the Neotropical genera as part of the world generic revision begun in Carpenter and Cumming (1985), take up the project. The opportunity is taken here to include lectotype designations for the Polistinae and species described in the genera *Montezumia* and *Monobia.* Notes are also provided on specimens of *Zethus* not seen by Bohart and Stange.

Most of the specimens in the collection bear small printed labels indicating only the locality and the month of collection. Single specimens described by Fox as new species generally bear a label in Fox's handwriting, giving the name and the indication "type". Of new species based on two or more specimens, as a rule only one specimen bears a type label. Some specimens have a yellow label giving the name and appellation "type", but the handwriting is unrecognized. These may be specimens previously sent to Bequaert for study and returned. Syntype specimens retained in the MCZ were labelled in Bequaert's handwriting as "paratype" or "cotype".

In the present paper lectotypes are designated for all the species based on two or more specimens. Generally we have selected as lectotype the specimen bearing Fox's original label, but in a few cases it appeared desirable to deviate from this rule, as explained in such instances below. The remaining specimens of a series have been marked as paralectotypes. In a few cases, Fox described variants, primarily based on color, with the term "Var.". We have not designated any such specimens as lectotypes, following Article 72(b) (i) of the current International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985*a*), which excludes specimens described as variants from the type series. This also applies to specimens doubtfully attributed to a species. We have labelled such specimens as paralectotypes, with a notation indicating their status. We have also attached holotype labels to the specimens of species based on unique specimens. The order of species follows that in Fox's papers.

We give here some information on the type localities. In addition to Fox (1896), we have consulted Papavero (1973:377–380), who traced some of the localities not found on modern maps or in gazeteers. These papers should be referred to for more complete information.

Santarem: 2°26′S, 54°42′W, town in Amazonas at the junction of the Tapajós and Amazon rivers. Most of the Hymenoptera labelled Santarem were collected a few miles inland in campo (savanna) habitat, or at settlements in heavy forest down the Amazon (Fox, 1896). **Mararú** is one of these settlements (spelled Marurú by Fox, 1896).

Rio de Janeiro: land originally forest; all specimens collected below 2500 ft altitude (Fox, 1896).

Corumbá: 19°1′S, 57°39′W, town in Matto Grosso on the western bank of the Paraguay, near the border with Bolivia; climate dry and hot and vegetation open (dry forest, full of cacti and other thorny plants). Specimens labelled "lowland" were collected on the opposite side of the river in a semi-swampy floodplain (Fox, 1896). The floodplain was mostly open grassland, with some gallery forest (Papavero, 1973:380.

Pedra Branca (Piedra Blanca), Bolivia: four miles west of Corumbá, near Lake Jacadigo; damp lowland covered with heavy forest (Fox, 1896).

Chapada: 15°26′S, 55°45′W, Matto Grosso; stretches of open land and semi-forest, interspersed with large patches of heavy forest; climate never very warm. Here the greater part of the collection was made, mainly on flowers and in muddy places near the streams (Fox, 1896). The town is now known as Chapada dos Guimarâes (Papavero, 1973:379), and the collections were made at elevations ranging from 1500 to 2500 ft.

Uacarizal was not listed in Fox (1896). It apparently was a plantation in Mato Grosso near either the Río Paraguay or Cuyabá, probably the former (Papavero, 1973:380).

SPECIES DESCRIBED OR LISTED IN THE POLISTINAE

Mischocyttarus

1. *Mischocyttarus labiatus* (Fabricius); Fox, 1898:445, "About 50 specimens", 43 specimens are present from Rio de Janeiro; Mararú; Chapada; Uacarizal; Pedra Branca.

Apoica

1. *Apoica pallida* (Olivier); Fox, 1898:445, "15 specimens", 14 are present; two, Rio de Janeiro and six, Chapada, January–April, =*A. gelida* Vecht; one, Chapada, October, =*A. flavissima* Vecht; four, Santarem, September and October, =*A. thoracica* Buysson; one, Santarem, =*A. pallens* (F.).

Synoeca

1. *Synoeca testacea* Saussure; Fox, 1898:446, eight specimens from Mararú and Santarem, =*S. virginea* (Fabricius) (synonymy by Richards, 1978:182).
2. *Synoeca surinama* (Linnaeus); Fox, 1898:446, "A large series", 68 specimens are present from Chapada; Uacarizal; Rio de Janeiro; Santarem.

Here also belongs the male (Uacarizal, February) discussed by Fox as "very close to *surinama*". It bears a label in his hand "*Synoeca* n. sp.?".

3. *Synoeca cyanea* (Fabricius); Fox, 1898:446, two specimens from Rio de Janeiro.
4. *Synoeca azurea* Saussure; Fox, 1898:446, one specimen from Chapada, =*S. surinama* (L.), misidentification.

Polistes

1. *Polistes ferreri* Saussure; Fox, 1898:446, "A large series", 49 specimens are present from Corumbá and Chapada. Another 35 specimens from Chapada, Santarem, and Rio de Janeiro, =*P. lanio* (F.); 12 specimens from Corumbá, Chapada and Uacarizal, =*P. canadensis* (L.); misidentifications.
2. *Polistes bicolor* Lepeletier; Fox, 1898:446, two specimens from Santarem, =*P. occipitalis* Ducke (synonymy by Bequaert, 1937:186).
3. *Polistes versicolor* (Olivier); Fox, 1898:446, "About 75 specimens", 76 specimens are present from Benevdes; Mararú; Rio de Janeiro; Chapada; Santarem.
4. *Polistes carnifex* (Fabricius); Fox, 1898:447, nine specimens recorded from Chapada; Rio de Janeiro; Corumbá; Santarem. Six specimens are present.
5. *Polistes cinerascens* Saussure; Fox, 1898:447, ten specimens are present from Chapada and Rio de Janeiro.
6. *Polistes pacificus* Fabricius; Fox, 1898:447, six specimens are present from Mararú and Santarem.
7. *Polistes acteon* [! =*actaeon*] Haliday; Fox, 1898:447, one specimen from Rio de Janeiro.
8. *Polistes subsericeus* Saussure; Fox, 1898:447, 16 specimens recorded from Chapada. Fourteen specimens are present. In the MCZ there is a male with the same locality and date labels, which apparently is from this series.
9. *Polistes thoracicus* Fox, 1898:447, described from six specimens, Chapada, February to April. Lectotype female, Chapada, March, CMNH, by present designation. Additional material in the CMNH includes two females, Chapada, March; one male, Chapada, April; one female with a handwritten Chapada label and no date (paralectotypes). One of the March females, which lacks the metasoma, is labelled by Bequaert "cotype". Fox did not mention a male, as noted by Bequaert (1937:174), who suggested the worker sign in Fox's description was an error for a male sign. It is the male which is labelled by Fox with the determination and the word "Types", but selection of a female as lectotype seems less likely to cause confusion regarding Fox's description. Bequaert mentioned seeing only five cotypes. In the MCZ there is a female from Chapada, February, labelled by Bequaert a "paratype" of this species. This is apparently a syntype, and we have labelled it paralectotype. It is perhaps possible that the specimen with the handwritten label was not part of the syntypic series, but other specimens undoubtedly seen by Fox bear such labels, so it seems more likely that the sixth syntype was never sent to Bequaert.

   Richards (1978:533) incorrectly stated that the "holotype" of this species is deposited in the Academy of Natural Sciences in Philadelphia.
10. *Polistes geminatus* Fox, 1898:448, described from two specimens, Chapada, March. Lectotype female, Chapada, March, CMNH, by present designation. In the MCZ there is a female, labelled by Bequaert "*Polistes geminatus* Fox

paratype 'var. of Fox' " with the same locality and date labels. This specimen corresponds to Fox's description of the "Var.", and so is apparently the second syntype. We have labelled it paralectotype.

Polybia

1. *Polybia fulvofasciata* (DeGeer); Fox, 1898:448, 43 specimens recorded from Chapada. Thirty-four specimens are present, =*Agelaia fulvofasciata,* new combination (generic nomenclature following Carpenter and Day, 1988).
2. *Polybia fasciata* Lepeletier; Fox, 1898:448, "About 100 specimens", 100 specimens are present from Chapada, =*P. emaciata* Lucas (synonymy by Richards, 1978:117).
3. *Polybia fastidiosuscula* Saussure; Fox, 1898:448, "Over 100 specimens", 121 specimens are present from Chapada. Six collected in October were sent to Bequaert, who labelled them as a variety with a manuscript name, and retained two specimens in the MCZ. These specimens have most of the second metasomal tergum yellow, but are otherwise typical.
4. *Polybia surinamensis* Saussure; Fox, 1898:448, 16 specimens recorded from Rio de Janeiro; Mararú; Santarem. Ten specimens are present, =*Mischocyttarus surinamensis.* An additional specimen (Rio de Janeiro, July) is in the MCZ. Another specimen from Santarem =*M. synoecus* Richards, and a further specimen from Santarem =*M. lecointei* (Ducke).
5. *Polybia occidentalis* (Olivier); Fox, 1898:449, "About 250 specimens of typical *occidentalis,* and over 60 representing *pygmaea* Fabr.", 244 and 20 specimens, respectively, are present from Chapada; Santarem; Rio de Janeiro. Some of these specimens are dated November, which was not mentioned by Fox. Fox also alluded to "Quite as large a series of individuals, having the head reddish", which he stated was not distinct as a species from typical *occidentalis.* There are 26 specimens from Chapada corresponding to this description, =*P. ruficeps* Schrottky. An additional six specimens of this latter species are present from Corumbá, but this locality was not mentioned by Fox.
6. *Polybia oecodoma* Saussure; Fox, 1898:449, six specimens recorded from Rio de Janeiro and Chapada. Five specimens are present, =*P. fastidiosuscula* Saussure, misidentification. The other specimen (Chapada, November) is in the MCZ, determined as *fastidiosuscula* by Bequaert.
7. *Polybia scutellaris* (White); Fox, 1898:449, "Nearly 100 specimens", 83 specimens are present from Chapada, =*P. erythrogaster* Richards. These are labelled by Fox as "*scutellaris* var.", and determined by Bequaert as *P. ruficeps* Schrottky. Fox stated that 90% of the specimens "represent a variety with the head and part of the thorax above, rusty-red", and several of the specimens have the scutum black, which was apparently not the case for the type series of *erythrogaster* (Richards, 1978:77). There is another specimen, with Fox's label, which is *scutellaris.* However, this is from "Rio Paraná, below Rozario", which is in Argentina. This cannot have been part of the original series, and perhaps the label was switched (the specimen was also labelled by Bequaert).
8. *Polybia pumila* Saussure; Fox, 1898:449, "About 100 specimens", 107 specimens are present from Chapada and Sebastiae, =*Protopolybia sedula* (Saussure) (synonymy by Richards, 1978:150). One of the Chapada, October, specimens is labelled by Bequaert with a manuscript name as the holotype of a variety of *Protopolybia rotundata.* Two additional specimens (Chapada, Sep-

tember and October) are in the MCZ; one is labelled "*Polistella pumila* Sauss." by Bequaert.

9. *Polybia pediculata* Saussure; Fox, 1898:449, "Over 60 examples", 52 specimens are present; 50 Chapada =*Metapolybia aztecoides* Richards; two, Santarem, =*M. unilineata* (Ihering).
10. *Polybia rejecta* (Fabricius); Fox, 1898:449, "About 50 specimens", 43 specimens are present from Mararú; Chapada; Santarem; Sebastiae.
11. *Polybia jurinei* Saussure; Fox, 1898:449, "Over 60 examples", 56 specimens are present from Chapada; Rio de Janeiro; Mararú; Santarem.
12. *Polybia metathoracica* Saussure; Fox, 1898:449, three specimens from Chapada; Mararú; Santarem, =*Mischocyttarus metathoracicus.*
13. *Polybia bifasciata* Saussure; Fox, 1898:449, two specimens from Santarem.
14. *Polybia rufidens* Saussure; Fox, 1898:450, one specimen from Corumbá, April, and one from Chapada, May. One female in the CMNH is the holotype of *Mischocyttarus metathoracicus* var. *picturatus* Bequaert, 1938*a*; the other, paratype female is in the MCZ (Bequaert, 1938*a*). Richards (1978:307) suggested that *picturatus* was a synonym of nominotypical *metathoracicus,* but recommended that the holotype (stated to be in MCZ) be re-examined.

    Examination of these specimens shows: (1) The holotype is not a synonym of *metathoracicus,* but a valid species, *M. picturatus* Bequaert, new status; (2) the paratype is not the same species, but is a specimen of *M. bertonii* Ducke, misidentification.

    Bequaert (1938*a*:135) gave the label data as Corumbá for the holotype and Chapada for the paratype. This is an error; the respective type labels are attached to the opposite specimens. That it is a reporting error, and not a label mix-up, seems apparent from the fact that the description does not correspond to the holotype, but rather to the paratype. The pronotum, upper corner of the mesepisternum and lower plate of the metapleuron are described as reddish, but they are black in the holotype. Also, most of the vertex is blackish, not just the ocellar area. Presumably, the detailed description was prepared after the holotype had been returned to the CMNH.

    The specimens both represent species in the subgenus *Kappa* Saussure, but differ in several important characters, in addition to color. The holotype (*M. picturatus*) has the occipital carina quite weak, the pronotal carina transversely straight, the mesepisternum dull with punctation uniform, the propodeal concavity shallow with the longitudinal medial carina strong ventrally, the propodeal valvulae broadly triangular posteriorly, and metasomal tergum I wider. The paratype (*M. bertonii*) has the occipital carina strong, the pronotal carina posteriorly concave in dorsal view, the mesepisternum shiny with distinct macropunctures interspersed among micropunctures, the propodeal concavity deep with the longitudinal medial carina effaced, the propodeal valvulae very short and straight in lateral view, and metasomal tergum I narrower and relatively more dilated apically.

    In Richards' (1978:289–292) key, *M. picturatus* keys to couplet 16, but comes from a different locality and does not correspond to the description of any of the other three species falling here. Using the descriptions in Richards, these four species all differ in color from *M. picturatus,* which has the entire clypeus and frons reddish, the tegula with a posteromesal spot, and the wings hyaline, contrasting with the other species. In addition, compared to

M. villarricanus Zikán (known only from Villarrica, Paraguay), the coloration of the head is reddish, not red-brown; the clypeus has some macropunctures; the pronotal carina is not "concave anteriorly"; the hindtibial spurs are yellowish at the tips; and the meso- and metasoma are not suffused with red. Compared to *M. funerulus* Zikán (known only from Rio de Janeiro, Itatiaia), the clypeus has some macropunctures dorsally; the pronotal carina is not "rather strong, a little concave anteriorly"; and the hindtibial spurs are yellowish only at the tips. Compared to *M. mocsaryi* (Ducke) (known only from Pará, Obidos), the mesepisternal punctation is not "almost honey-comb like"; and the hindtibial spurs are partly brownish.

The paratype keys to couplet 20 in Richards (1978). Its metasoma is not really reddish brown, as stated in couplet 19, but neither is the metasoma in specimens of *M. bertonii* examined, including the paratype in the MCZ seen by Richards (1978:301). The mesepisternal punctation and propodeal valvulae match the species in the *injucundus* group, while the pronotal carina and propodeal concavity match *bertonii.* The head and mesosoma are somewhat more reddish than other specimens examined or described, but this does not seem significant compared to the correspondence in other features.

15. *Polybia atra* (Olivier); Fox, 1898:450, "About 250 examples", 253 specimens are present from Chapada and Santarem, =*P. ignobilis* (Haliday) (synonymy by Bequaert, 1943*c*:718; Richards, 1978:106). An additional specimen (Chapada, March) is in the MCZ, labelled "*nigra* Sss." by Bequaert, an additional junior synonym of *ignobilis.*
16. *Polybia dimidiata* (Olivier); Fox, 1898:450, 34 specimens from Chapada. Thirty-three specimens are present. A further male specimen is in the MCZ, labelled by Bequaert.
17. *Polybia socialis* Saussure; Fox, 1898:450, one specimen from Rio de Janeiro, =*Mischocyttarus atramentarius* Zikán (synonymy by Richards, 1978:298).
18. *Polybia sylveirae* Saussure; Fox, 1898:450, three specimens from Rio de Janeiro. Two specimens are present, =*Protonectarina sylveirae.* The other specimen is in the MCZ, labelled by Bequaert.
19. *Polybia pallipes* (Olivier); Fox, 1898:450, "About 45 specimens", three specimens are present from Santarem, =*Agelaia pallipes* (Olivier), new combination (generic nomenclature following Carpenter and Day, 1988). The following are all misidentifications in the original series. Twenty-nine specimens from Chapada, Corumbá, Pedra Branca, Mararú, Santarem, and "Brazil", =*Agelaia multipicta* (Haliday), new combination. Three specimens from Rio de Janeiro, =*Agelaia myrmecophila* (Ducke), new combination. Eight specimens from Chapada, =*Agelaia myrmecophila* or a species near; the first metasomal segment is shorter and broader than other *myrmecophila.* One specimen from Santarem, =*Polybia bistriata* (F.). One specimen from Chapada, =*Mischocyttarus cerberus* Ducke, typical color pattern.
20. *Polybia vespiceps* Saussure; Fox, 1898:450, "About 60 specimens", 59 specimens are present from Sebastiae and Chapada, =*Pseudopolybia vespiceps.* Three specimens (Chapada, October and March; Sebastiae) labelled "*testacea*" (a variety of *vespiceps*) by Bequaert in the MCZ may also be from this series. Fox did not report any dates for the Chapada material.
21. *Polybia liliacea* (Fabricius); Fox, 1898:450, "A large series", 13 specimens are present from Santarem and Mararú. An additional 88 specimens from

Chapada and Santarem, =*P. striata* (F.); misidentification. Two further specimens (Chapada, March and April) in the MCZ were determined by Bequaert as *P. striata.*

21. *Polybia angulata* (Fabricius); Fox, 1898:450, 11 specimens from Santarem. Ten specimens are present, =*Agelaia angulata* (F.), new combination (generic nomenclature following Carpenter and Day, 1988).
22. *Polybia carbonaria* Saussure?; Fox, 1898:450, one male from Rio de Janeiro. The nominal species is now placed in the subgenus *Clypeopolybia* of *Mischocyttarus.* However, this specimen is misidentified. It belongs in the subgenus *Megacanthopus,* and is evidently an undescribed species. It has the characteristic anterior pronotal flange of *Megacanthopus,* and the terminal antennal flagellomere is flattened and more or less truncate. The mandibles have a small fourth tooth, unlike the other species in this subgenus (Richards, 1978).
23. *Polybia angulicallis* [! =*angulicollis*] (Spinola); Fox, 1898:450, two specimens from Santarem, =*Agelaia angulicollis* (Spinola), new combination (generic nomenclature following Carpenter and Day, 1988).
24. *Polybia lugubris* Saussure; Fox, 1898:450, one specimen from Rio de Janeiro. This specimen is labelled as *P. flavitincta* Fox by Bequaert, but Fox's identification is correct.
25. *Polybia flavicans* (Fabricius); Fox, 1898:451, 18 specimens from Mararú and Santarem, determined as "*Polybia flavicans* Fabr. (=*testacea* Fabr.)". Sixteen specimens are present, =*Agelaia testacea* (F.), new combination (generic nomenclature following Carpenter and Day, 1988). Fox followed Saussure (1854: 183) in treating *flavicans* and *testacea* as synonyms. The former species is now placed in the genus *Mischocyttarus.*
26. *Polybia paraensis* Saussure; Fox, 1898:451, five specimens from Mararú and Santarem. Four specimens are present, =*Angiopolybia paraensis.* A further specimen (Santarem) is in the MCZ, labelled by Bequaert.
27. *Polybia chrysothorax* (Lichtenstein); Fox, 1898:451, "About 40 specimens", 42 specimens are present from Chapada and Santarem.
28. *Polybia sericea* (Olivier); Fox, 1898:451, "Nearly 200 specimens from various localities", 173 specimens are present.
29. *Polybia mexicana* Saussure?; Fox, 1898:451, four specimens from Rio de Janeiro; three females =*Mischocyttarus adjectus* Zikán, one male =*M. parallelogrammus* Zikán.

    Mischocyttarus adjectus was hitherto known only from the holotype, which has not been examined. Zikán described three species from Rio de Janeiro, Itatiaia, which are separated in Richards' (1978:282) key by the form of the pronotal carina. These three specimens are actually somewhat variable in this feature: only one has a clear raised central angle, but the other two approach this. It is possible that there are fewer species than described.
30. *Polybia infernalis* Saussure; Fox, 1898:451, two specimens from Santarem, =*P. bistriata* (Fabricius), misidentification.
31. *Polybia emaciata* Lucas; Fox, 1898:451, 12 specimens from Mararú and Santarem. Seven specimens are present, =*Angiopolybia pallens* (Lepeletier), misidentification.
32. *Polybia sedula* Saussure; Fox, 1898:451, "Over 75 specimens", 87 specimens are present from Chapada, Mararú, and Sebastiae, =*Protopolybia exigua* (Saussure) (synonymy by Richards, 1978:142). A further specimen (Chapada, October) is in the MCZ, labelled "*sedula*" by Bequaert.

33. *Polybia latior* Fox, 1898:451, described from three specimens, Chapada, October, =*Mischocyttarus latior.* Lectotype female, Chapada, October, CMNH, by present designation. Additional material in the CMNH is one female with a handwritten locality label and without a date label (paralectotype). It is the latter specimen that bears Fox's determination label and the word "Types", but we are selecting the specimen with more complete label data as lectotype. In the MCZ is another female labelled by Bequaert as "cotype", apparently the other syntype, which we have labelled paralectotype.

    Richards (1978:294) erroneously stated that the "holotype" of this species is deposited in the Academy of Natural Sciences in Philadelphia.
34. *Polybia flavitincta* Fox, 1898:452, described from two specimens, Santarem. Lectotype female, Santarem, CMNH, designated by Richards (1978:113), who incorrectly gave the depository as the Academy of Natural Sciences in Philadelphia. Additional material in the CMNH includes the paralectotype female. Both specimens are labelled by Bequaert as synonym of *P. mediamericana* Bequaert.
35. *Polybia tinctipennis* Fox, 1898:452, described from two specimens, Chapada, September and December. Lectotype female, Chapada, September, CMNH, by present designation. The female from December is now in the MCZ, labelled by Bequaert as "cotype". We have labelled it as paralectotype.

    Richards (1978:103) erroneously listed the "holotype" of this species as deposited in the Academy of Natural Sciences in Philadelphia.
36. *Polybia chapadae* Fox, 1898:453, described from three specimens, Chapada, February, =*Mischocyttarus chapadae.* Lectotype female, Chapada, February, CMNH, by present designation. Additional material in the CMNH includes a second female (paralectotype). The third syntype is now in the MCZ (paralectotype female).

    Richards (1978:331) studied the MCZ syntype of this species, and incorrectly stated that the other types are deposited in the Academy of Natural Sciences in Philadelphia.
37. *Polybia gorytoides* Fox, 1898:454, described from 12 females, Chapada, September, and Santarem. Lectotype female, Chapada, September, CMNH, by present designation. Additional material in the CMNH includes three females, Chapada, September; four females, Santarem (paralectotypes). There is also one female from Chapada, December, which may not be part of the type series, since Fox did not mention this date. We have nevertheless labelled it paralectotype. In the MCZ is another female from Chapada, September, labelled by Bequaert as "cotype", which we have labelled paralectotype.

    Richards (1978:102) erroneously listed the "holotype" of this species as deposited in the Academy of Natural Sciences in Philadelphia.
38. *Polybia suffusa* Fox, 1898:455, described from "About 60 specimens", Chapada, May and October, =*Metapolybia suffusa.* Lectotype female, Chapada, October, CMNH, by present designation. Additional material in the CMNH includes 38 females, October, and 23 females, May (paralectotypes). Another specimen collected in May is now in the MCZ, labelled by Bequaert "cotype" (paralectotype).

    Richards (1978:188) erroneously listed the "holotype" of this species as deposited in the Academy of Natural Sciences in Philadelphia.
39. *Polybia frontalis* Fox, 1898:455, described from "Ten females (workers?), one male", Chapada, October and November, =*Mischocyttarus frontalis.* Lectotype female, Chapada, October, CMNH, by present designation. Additional

material in the CMNH includes eight females, Chapada, October (paralectotypes). In the MCZ are one female (November) and two males (October and no date), labelled by Bequaert as "cotype" or "paratype" (paralectotypes). The male without a date label has a handwritten locality label by Bequaert, and is possibly not a syntype. However, Fox's count may have been incorrect.

Richards (1978:296) incorrectly stated that the types are deposited in the Academy of Natural Sciences in Philadelphia.

40. *Polybia marginata* Fox, 1898:456, described from four specimens, Chapada, September and October, =*Mischocyttarus marginatus.* Lectotype female, Chapada, September, CMNH, by present designation. Additional material in the CMNH includes one female, October, and one female without date label (paralectotypes). Another female collected in October is now in the MCZ, labelled by Bequaert "cotype" (paralectotype).

Richards (1978:326) incorrectly stated that the types are deposited in the Academy of Natural Sciences in Philadelphia.

Tatua

1. *Tatua morio* (Fabricius); Fox, 1898:457, "About 40 specimens", 41 specimens are present from Chapada and Santarem, =*Epipona tatua* (Cuvier).

As pointed out by Bequaert (1938*b*:115), *Tatua* Saussure, 1854, was proposed as a replacement name for *Epipona* Latreille, 1802, under the incorrect impression that *Epipona* was preoccupied (by Latreille, not Kirby as stated by Bequaert). Bequaert himself overlooked that Blanchard (1840:394) had designated *Vespa morio* Fabricius, 1798, as the type species of *Epipona,* the same species Ashmead (1902:166) designated as the type species of *Tatua.* The latter name is thus a junior objective synonym, as noted by Bequaert (1943*b*:4). The synonymy of *V. morio* F. with *V. tatua* Cuvier, 1797, was pointed out by Dalla Torre (1904:82).

Chartergus

1. *Chartergus apicalis* (Fabricius); Fox, 1898:457, "Over 60 specimens", 50 are present from Sebastiae; Chapada; Corumbá; Mararú; =*Parachartergus fraternus* (Gribodo). Another specimen (Chapada, October) is in the MCZ, labelled "*Parachartergus apicalis* var. *fraternus* Grib." by Bequaert.
2. *Chartergus smithii* Saussure; Fox, 1898:457, one specimen from Corumbá, =*Parachartergus smithii.*
3. *Chartergus ater* Saussure; Fox, 1898:457, two specimens from Chapada and Santarem. The specimen from the former locality is now in the MCZ.

These two specimens, along with a female from "Anapolis, Goyaz (G. Fairchild)" in the MCZ, were all the material seen by Bequaert (1938*b*:111) when he described the monotypic subgenus *Chartergellus* for *Vespa frontalis* Fabricius, 1804. He treated *Chartergus ater* Saussure, 1854, as a synonym, following Ducke (1910). Bequaert also noted that this latter name was preoccupied by *Chartergus ater* Lepeletier, 1836, a synonym of *Parachartergus apicalis* (F.).

Chartergellus was raised to generic rank by Richards (1978), who noted that *Vespa frontalis* F. was itself preoccupied by *Vespa frontalis* Latreille, 1802, a synonym of *Dolichovespula sylvestris* Scopoli, 1763. Ducke (1910) had treated *Chartergus zonatus* Spinola, 1851, as a synonym of *V. frontalis* F., but Richards did not follow this. He described four new species of *Char-*

tergellus and, although not seeing the type of *Chartergus zonatus,* stated that the description did not resemble any specimens he had seen, and treated this taxon as *incertae sedis.* He proposed *Chartergellus amazonicus* as a replacement name for *V. frontalis* F., which he thus considered the name of the type species of the genus.

Richards (1978:217) suggested that *V. frontalis sensu* Bequaert was probably a mixture of species, and implied that this rendered tentative his treatment of *C. amazonicus* as the type species. In fact, all of the specimens studied by Bequaert are *Chartergellus communis* Richards, but this is irrelevant to the question of the type species. Bequaert's designation of *V. frontalis* could only be affected if it were considered that he had misidentified this species (Article 70 of the Code). His subgenus was monotypic for the nominal species. Hence, it is unaffected by the uncertain status of *Chartergus zonatus,* since he regarded that as a synonym (Article 69(d)). Plainly, Richards' subsequent description of new species from material that formerly was considered one taxon also does not affect Bequaert's identification (Article 17).

4. *Chartergus chartarius* (Olivier); Fox, 1898:457, "Nearly 50 specimens", 44 specimens are present from Chapada and Santarem. Two additional specimens (Chapada, October) are in the MCZ.
5. *Chartergus globiventris* Saussure; Fox, 1898:457, two specimens from Sebastiae.
6. *Chartergus fasciatus* Fox, 1898:457, one female, Mararú, April (holotype), =*Parachartergus smithii* (Saussure), new status. Richards (1978) did not include *fasciatus* in his synonymy or key. Bequaert (1938*b*:111) treated it as a variety of *smithii,* stating that "I cannot detect on the type the differences mentioned by Fox", but noted that the color is distinctive. He also recorded a second specimen from Pirapora, Minas Gerais. This specimen is in the MCZ, and comparison of it and the holotype of *fasciatus* with typical *smithii* confirms that the proportions of the mesosomal dorsal sclerites do not differ, contrary to Fox. Bequaert stated that the forewing was more infuscated, but *smithii* is quite variable in this regard; for example, specimens in the MCZ from Tingo Maria, Peru, have the forewings as dark as in *fasciatus.* And whereas the first three metasomal terga are darker than in typical *smithii,* there is variation in this as well. The first tergum is often quite dark, and the second tergum is often somewhat darker basally than apically. We regard the color differences as trivial, and treat *fasciatus* as a synonym of *smithii.*
7. *Chartergus griseus* Fox, 1898:458, described from nine specimens, Mararú, April, and Santarem, =*Parachartergus griseus.* Lectotype female, Santarem, CMNH, by present designation. Additional material in the CMNH includes five females, Santarem; two females, Mararú, April (paralectotypes). Another female (Santarem) is now in the MCZ, labelled by Bequaert "cotype" (paralectotype).

   Richards (1978:213) incorrectly stated that the types are deposited in the Academy of Natural Sciences in Philadelphia.

Charterginus

1. *Charterginus fulvus* Fox, 1898:458, 459, described from eight specimens, Mararú, April, and Santarem. Lectotype female, Santarem, CMNH, by present designation. Additional material in the CMNH includes six females, Santarem (paralectotypes). There is also a specimen from Santarem, Novem-

ber, labelled in an unrecognized hand as "type", which is perhaps not a syntype, as Fox did not mention any date for this locality. We have, however, labelled it paralectotype. Richards (1978:131) stated that a "paratype" is now in the British Museum, and in the MCZ there is a female labelled by Bequaert as from Santarem and "paratype", which we have labelled paralectotype. It seems likely that Fox's count was incorrect.

2. *Charterginus fuscatus* Fox, 1898:459, one female, Mararú, April (holotype), =*Protopolybia fuscatus,* new combination (generic placement following Ducke, 1905:15; nomenclature following Carpenter and Wenzel, 1990).
3. *Charterginus cinctellus* Fox, 1898:459, described from seven specimens, Chapada, October, =*Protopolybia chartergoides* (Gribodo), new combination (generic placement following Ducke, 1907:161; nomenclature following Carpenter and Wenzel, 1990). Richards (1978:155–156) treated this taxon as a "morph" of *chartergoides,* which is a category without nomenclatural standing. Lectotype female, Chapada, October, CMNH, by present designation. Additional material in the CMNH includes five paralectotype females. The specimen with Fox's type label is missing part of the metasoma, therefore we have selected an undamaged specimen as lectotype. In the MCZ is another female labelled by Bequaert "cotype", which is evidently the remaining syntype (paralectotype).

Nectarinia

1. *Nectarinia lecheguana* (Latreille); Fox, 1898:459, "About 50 specimens", 53 specimens are present from Chapada; Corumbá; Santarem; =*Brachygastra lecheguana.*

   Nectarinia is an incorrect spelling of *Nectarina* Swainson and Shuckard, 1840, an unnecessary replacement name for *Brachygastra* Perty, 1833, which was erroneously thought to be preoccupied by *Brachygaster* Leach, 1830. *Brachygastra* has been used as the valid name for this genus since 1943 (Bequaert, 1943*a*:303).
2. *Nectarinia bilineolata* Spinola; Fox, 1898:459, 35 specimens from Chapada. Thirty-four specimens are present, =*Brachygastra moebiana* (Saussure), misidentification. These specimens were also labelled by Naumann as *bilineolata.*
3. *Nectarinia augusti* Saussure; Fox, 1898:459, 25 specimens from Chapada and Santarem, =*Brachygastra augusti.*
4. *Nectarinia scutellata* Spinola; Fox, 1898:459, one specimen from Chapada, =*Brachygastra scutellaris* (Fabricius) (synonymy by Ducke, 1905:11).

SPECIES DESCRIBED OR LISTED IN THE EUMENINAE

Zethus

1. *Zethus prominens* Fox, 1899:408, described from four specimens from Chapada, March, April. Bohart and Stange (1962:31) studied two females, one of which was designated as lectotype. The other, which they termed "Topotypical lectoparatype", was listed as being in the MCZ but it is not. In Bohart and Stange (1965:36) it is listed as being in the collection of the University of California at Davis.
2. *Zethus striatifrons* Fox, 1899:409, described from seven females and two males from Chapada, March, October and December. Bohart and Stange (1962:32) designated one male as lectotype, and mentioned four female "To-

potypical lectoparatypes". One of these was listed as being in the MCZ, where there is also a male, labelled by Bequaert as "paratype" and Bohart and Stange as "lectoparatype".

3. *Zethus rufipes* Fox, 1899:411, described from an unspecified number of males, Chapada, January and March. Bohart and Stange (1962:31) mentioned three males, one of which they designated lectotype. A "Topotypical lectoparatype" was stated to be in the MCZ, but is not there. This species was omitted from Bohart and Stange (1965).
4. *Zethus campanulatus* Fox, 1899:415, described from five females and one male from Chapada, March. Bohart and Stange (1962:29) designated as lectotype one female, and alluded to four females "Topotypical lectoparatypes". In Bohart and Stange (1965:50) they indicated that they had studied only four females. There are one female and one male at the CMNH, labelled with a note: "By oversight never card-catalogued; never sent to R M Bohart GEW—1974". They have the same date/locality labels as the type series; the female also has a handwritten label "*campanulatus* Fox types", which the male is labelled by Bequaert "prob. not true male of *campanulatus* Fox". We have labelled these specimens as paralectotypes.
5. *Zethus ? ferrugineus* Saussure; Fox, 1899:421, four specimens from Santarem. Bohart and Stange (1965:184) did not state how many specimens they saw from the CMNH. There are two in the collection that are possibly part of the original material, =*Z. biglumis ferrugineus.*
6. *Zethus proximus* Fox, 1899:422, described from one female, Corumbá, April; and one male, Uacarizal, February. The female was seen by Bohart and Stange (1962:31), who designated it as lectotype. A male in the CMNH from Uacarizal is labelled "*proximus* Fox type" and "By oversight never card-catalogued; never sent to R. M. Bohart GEW—1974". We have labelled it as paralectotype.

Labus

1. *Labus brasiliensis* Fox, 1899:434, described from one female, Chapada, September; and one male, Santarem. The female was seen by Bohart and Stange (1962), who designated it as lectotype (1965:113). A male in the CMNH from Santarem is labelled "*Labus brasiliensis* Fox type" and "This is prob. *not* the spmn that was card-catalogued in 1941 (GW 1974)". We have labelled it as paralectotype. *Labus brasiliensis* Fox is a junior secondary homonym of *Zethus brasiliensis* Saussure, 1853, and the name has been replaced by *Z. adonis* Bohart and Stange (1965:113).

Eumenes

1. *Eumenes chrysothorax* Saussure; Fox, 1899:437, one male, Corumbá, April, =*Pachymenes sericeus* Saussure (synonymy by Giordani Soika, 1990:96).
2. *Eumenes sericea* Saussure; Fox, 1899:437, two females, Corumbá, April; two females, Santarem; =*Pachymenes ghilianii* (Spinola), misidentification. One of the Santarem specimens is labelled in Bequaert's handwriting "*Eumenes pallipes* Saussure (called *sericea* by Fox)". *Pachymenes pallipes* Saussure (1852: 75) was not originally described as a new species, but as a doubtful synonym of *Vespa pallipes* Olivier (a social wasp now in the genus *Agelaia*). Saussure (1855:153) indicated that *P. pallipes* was not a synonym, but Giordani Soika (1990:77) reduced this taxon to a synonym of *Pachymenes ghilianii* (Spinola).

3. *Eumenes bipartita* Fox, 1899:437, one female, Corumbá, April (holotype), =*Pachymenes bipartitus* (Fox) (generic placement by Giordani Soika, 1990: 76, 104). In the MCZ there is a male with the same locality and date labels, and labelled by Bequaert a "paratype" of this species. It does not seem to us likely that Fox would have overlooked a second specimen, and he did not describe the male. We therefore do not regard this specimen as part of the original type species. There is considerable topotypic material from Smith in the CMNH, deposited after Fox's publications, and we presume that this male is one of these specimens.
4. *Eumenes testacea* Fox, 1899:438, described from one female and two males, Santarem, =*Stenosigma testaceum* (Fox) (generic placement by Giordani Soika, 1990:148, 149). Lectotype male, Santarem, CMNH, by present designation. The lectotype bears a type label in Bequaert's handwriting. Giordani Soika (1990:149) referred to this specimen as "designato Lecto-olotipo del Van der Vecht"; we do not regard this as a valid lectotype designation. Additional material in the CMNH includes the paralectotype male and female. The paralectotype male is missing the terminal part of the metasoma. The female paralectotype is labelled by Fox "*Eumenes testacea* Fox Types", but in this case the male was described first and more completely. In the MCZ there is a female with the same locality and date labels, and labelled by Bequaert as a "paratype" of this species, but Fox only mentioned three specimens, and there seems to be no reason to regard this as part of the type series.
5. *Eumenes laevis* Saussure; Fox, 1899:439, six females, Santarem; two females, Pedra Branca; one female, Mararú; =*Santamenes santanna* (Saussure) (synonymy by Giordani Soika, 1990:117). Fox also mentioned Corumbá as a locality, but there are no specimens with this label.
6. *Eumemes* [!] *novarae* Saussure; Fox, 1899:439, one female, Chapada, December; four females and one male, Santarem; =*Santamenes novarae* (Saussure) (generic placement by Giordani Soika, 1990:117, 128). One of the Santarem females is labelled by Bequaert "*Eumenes novarae* Sauss. (Fox det.)".
7. *Eumenes insignis* Fox, 1899:439, described from two females and four males, Chapada, March, October, and November, =*Alphamenes insignis* (Fox). Lectotype female, Chapada, October, CMNH, by present designation. The lectotype bears a Fox type label. Additional material in the CMNH includes one female and one male, March; one male, November (paralectotypes). Giordani Soika (1978:332, 355, 357) examined the type series, but referred to the specimens only as "Lecto-paratipo".

   Giordani Soika (1978) recognized three subspecies of *insignis.* We have not examined specimens of *insignis richardsi* or *insignis loquax,* but their distinction was based solely on color, and we anticipate that their recognition will prove to be the same sort of partitioning of continuous variation demonstrated in the genus *Zeta* by Carpenter (1988).
8. *Eumenes laeviventris* Fox, 1899:440, described from two females and eight males, Corumbá, April, =*Pachymenes laeviventris* (Fox) (generic placement by Giordani Soika, 1990:76, 115). Lectotype female, Corumbá, April, CMNH, by present designation. The lectotype has a Fox type label. Giordani Soika (1990:115) referred to this specimen as "che il Van der Vecht designò Lecto-olotipo"; we do not regard this as a valid lectotype designation. Additional

material in the CMNH includes one female and eight male paralectotypes. A male and the female were labelled as types by Bequaert.

9. *Eumenes convexa* Fox, 1899:441, described from two specimens, Santarem, November, =*Alphamenes convexus* (Fox). Lectotype male, Santarem, November, CMNH, designated by Giordani Soika (1978:333, 347). Additional material in the CMNH includes a paralectotype male. Both specimens are damaged by dermestids: the lectotype has the apical antennal flagellomeres missing; the paralectotype has lost the head and prothorax. The paralectotype has Fox's type label, and the lectotype is labelled as type by Bequaert. Giordani Soika designated the lectotype by illustrating the less damaged specimen and referring to it as "lecto-olotipo" on pages 348 and 349. He did not label it because he was simply recording the specimens as labelled by van der Vecht. Nevertheless, his action takes precedence (Article 74 of the Code). We have appropriately labelled each specimen.
10. *Eumenes superficialis* Fox, 1899:441, described from one female and two males, Corumbá, April; Chapada, December; =*Pirhosigma superficiale* (Fox). Lectotype female, Chapada, December, CMNH, designated by Giordani Soika (1978:230, 236). Additional material in the CMNH includes two males, Corumbá, April (paralectotypes). Giordani Soika's lectotype designation was inadvertent, by referring to the female as "lecto-olotipo", and he did not label it. We have done so.

    Giordani Soika (1978) recognized two subspecies of *superficiale*. These "subspecies" are distinguished solely by the relative extent of the yellow apical bands on the metasomal segments, which moreover varies within *superficiale impurum,* as noted by Giordani Soika (1978:239). Examination of extensive series of both subspecies in the MCZ shows that this is trivial variation, and we herewith treat *P. superficiale impurum* Giordani Soika, 1978:230 (in key), 239, as a synonym of *P. superficiale* (Fox), new status.
11. *Eumenes usitata* Fox, 1899:442, described from one female and 12 males, Corumbá, April, May; Santarem; =*Alphamenes usitatus* (Fox). Lectotype female, Corumbá, April, CMNH, by designation of Giordani Soika (1978: 334, 345). Additional material in the CMNH includes five males, Corumbá, April; one male, Corumbá, May; one female and two males, Santarem (paralectotypes). Fox evidently mistook the sex of one of the males. One of the Corumbá, April males is labelled as type by Bequaert. An additional male paralectotype from Santarem =*A. campanulatus* (F.), misidentification. In the MCZ is one male from Santarem, which is apparently one of the other syntypes (paralectotype). It is labelled as *Eumenes usitatus* by Bequaert. Some paralectotypes are badly damaged. Giordani Soika's lectotype designation was inadvertent, when he referred to the Corumbá female as "lecto-olotipo", and he did not label it. We have done so.
12. *Eumenes incerta* Saussure; Fox, 1899:443, one female and two males, Rio de Janeiro, November, =*Alphamenes incertus* (Saussure) (generic placement by Giordani Soika, 1978:333, 350).
13. *Eumenes callimorpha* Saussure; Fox, 1899:444, recorded from seven specimens, "all females", Mararú;, April, and Santarem. Present are one female and two males, Mararú, April; one female and one male, Santarem; =*Alphamenes campanulatus* (Fabricius) (synonymy by van der Vecht, 1970:21; generic placement by van der Vecht, 1977:238, 242, 243). Van der Vecht

(1977) was overlooked by Giordani Soika (1978:334–342). In the MCZ is an additional specimen evidently from this series, a male from Santarem labelled by Bequaert "*Eumenes callimorpha* var. *incertus* Sauss." and determined by Giordani Soika as "*campanulatum incertum*". These are misidentifications; this specimen is *campanulatus.*

Giordani Soika (1978) recognized five subspecies of *campanulatus*: the nominotypical form; *A. c. mango* Giordani Soika, 1978:334 (in key), 342; *A. c. nanicolor* Giordani Soika, 1978:334 (in key), 343; *A. c. gladiator* Giordani Soika, 1978:334 (in key), 343; and *A. c. luctuosus* Giordani Soika, 1978:334 (in key), 344. The MCZ male is the nominotypical form. However, these "subspecies" are based solely on color differences, and their distributions overlap. Examination of four of these subspecies represented in the MCZ (including the holotypes of *mango* and *nanicolor*) confirms that these taxa represent partitioning of continuous variation, as was demonstrated in the genus *Zeta* by Carpenter (1988). We regard this practice as dubious, and herewith treat all of the subspecies as synonyms of *A. campanulatus* (Fabricius), new status.

14. *Eumenes picturata* Fox, 1899:444, described from two females and one male, "Pedra Branca and Corumbá, in April", =*Pachymenes picturatus* (Fox) (generic placement by Giordani Soika, 1990:75, 108). Lectotype female, Pedra Branca, April, CMNH, by present designation. Giordani Soika (1990:112) referred to this specimen as "scelta V. d. Vecht come Lecto-olotipo"; we do not regard this as a valid lectotype designation. Additional material in the CMNH includes one female, Pedra Branca, April; one male, Corumbá, April (paralectotypes). The female paralectotype and the male are labelled as types by Bequaert.
15. *Eumenes consobrina* Saussure; Fox, 1899:444, 14 specimens recorded from Corumbá, March, April; Rio de Janeiro, November. Present as one female and seven males, Corumbá, April; one female and one male, Rio de Janeiro, November; =*Cyphomenes anisitsii* (Brèthes), misidentification (according to Giordani Soika, 1978:211).

    Giordani Soika (1978) recognized two subspecies of *anisitsii,* and listed this series under the nominotypical form. We have not examined specimens of *anisitsii ornatissimus* Giordani Soika, but as before the distinction of these subspecies is based solely on color, so we regard their recognition as dubious.
16. *Eumenes parvula* Saussure; Fox, 1899:444, 14 specimens recorded from Corumbá, April, May; Chapada, January, April, December; Rio de Janeiro, November. Present are one female and one male, Corumbá, April; two males, Chapada, January; one male without label; =*Omicron minutum* (Fabricius) (synonymy by Giordani Soika, 1978:78). The Corumbá male is labelled by Bequaert "*Eumenes parvulus* Sauss. det. Fox". Giordani Soika determined the following three specimens evidently from this series as other species: one female, Corumbá, April, =*Omicron microscopicum* (Saussure); one male Chapada, April, labelled by Bequaert "*Eumenes parvulus* Sauss. det. Fox, =*Omicron nanum* (Kirsch); one female, Rio de Janeiro, November, =*Omicron spegazzinii* (Brèthes). None of these specimens was recorded by Giordani Soika (1978), and the first two are from localities well outside the distributions of the respective species reported by Giordani Soika.
17. *Eumenes suffusa* Fox, 1899:445, described from 11 females and three males, Corumbá, April; Chapada, November, December; =*Minixi suffusum* (Fox).

Lectotype female, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes six females and four males, Corumbá, April; one female, Chapada, November; one female and one male, Chapada, December (paralectotypes). One of the Corumbá females is labelled as type by Bequaert. Giordani Soika (1978:370, 379) referred to a female from Corumbá as "lecto-olotipo", but did not distinguish a specimen. However, this was undoubtedly the specimen labelled as lectotype by van der Vecht but not published.

18. *Eumenes uruguayensis* (!) Saussure [*recte uruguyensis*]; Fox, 1899:446, one female Chapada, December, one male, November, =*Minixi brasilianum compactum* (Fox) (according to Giordani Soika, 1978:375).
19. *Eumenes compacta* Fox, 1899:446, described from four females and one male, Corumbá, April; Chapada, November, December; =*Minixi brasilianum* (Saussure), new status. Lectotype female, Chapada, November, CMNH, by present designation. Additional material in the CMNH includes one female, Chapada, November; two females, Chapada, December; one male, Corumbá, April (paralectotypes). A December female and the male are labelled as types by Bequaert. Giordani Soika (1978:375) alluded to a female "lecto-olotipo" but did not specify the date or label the specimen. However, this was undoubtedly the specimen already labelled as lectotype by van der Vecht but not published.

    Giordani Soika (1978) treated *compacta* as a subspecies of *M. brasilianum.* The subspecies were separated by *compacta* having the mesosoma with reddish markings, while nominotypical *brasilianum* has the mesosoma black. However, the extent of reddish coloration varies considerably in *compacta,* and the MCZ male from Belém seen by Giordani Soika (1978:374) has a few small reddish marks. We do not believe that partitioning minor color variation into "subspecies" serves any useful purpose, and we treat *M. brasilianum compactum* as a synonym of *M. brasilianum.*
20. *Eumenes colorata* Fox, 1899:447, described from one female and one male, Chapada, September; Santarem; =*Pararhaphidoglossa colorata* (Fox). Lectotype female, Santarem, CMNH, by designation of Giordani Soika (1978: 263, 265, 323). Additional material in the CMNH includes the male, Chapada, September (paralectotype). The male is labelled as type by Bequaert. Giordani Soika's designation of the lectotype was inadvertent, when he referred to it as "lecto-olotipo". We have labelled the specimens appropriately.
21. *Eumenes tinctura* Fox, 1899:448, described from one female, Corumbá, April, and one male, Chapada, January; =*Pararhaphidoglossa tinctura* (Fox). Fox referred the male to this species "doubtfully". Lectotype female, Corumbá, April, CMNH, designated by Giordani Soika (1978:262, 264, 319). The paralectotype male is also in the CMNH. Giordani Soika's lectotype designation was inadvertent, when he referred to it as "lecto-olotipo". We have labelled the specimens appropriately.
22. *Eumenes invenusta* Fox, 1899:448, one female, Santarem (holotype), =*Pararhaphidoglossa invenusta* (Fox) (generic placement by Giordani Soika, 1978: 263, 301).
23. *Eumenes confluenta* Fox, 1899:449, described from one female and one male, Santarem, =*Pararhaphidoglossa confluenta* (Fox). The male was referred to this species "with much doubt". Lectotype female, Santarem, CMNH, designated by Giordani Soika (1978:259, 264, 268). The paralectotype male is

also in the CMNH. Giordani Soika's lectotype designation was inadvertent, when he referred to the types as "olotipo" and "allotipo". We have labelled the specimens appropriately.

Giordani Soika (1978) recognized two subspecies of *confluenta,* referring *simillima* Zavattari to this species. His key (1978:260) separates them using only color characters, however the single specimen of *simillima* examined, in the MCZ, is considerably smaller than the material of nominotypical *confluenta* we have seen. Giordani Soika gave measurements that overlapped, but the status of these taxa should be re-examined.

24. *Eumenes proxima* Fox, 1899:450, one female, Santarem (holotype), =*Pararhaphidoglossa proxima* (Fox) (generic placement by Giordani Soika, 1978: 260, 278).
25. *Eumenes cribrosa* Fox, 1899:451, described from six specimens, Mararú, April; Santarem; =*Omicron globicolle* (Spinola) (according to Giordani Soika, 1978:59, 177). Lectotype female, Santarem, CMNH, by present designation. Paralectotypes in the CMNH include one female, Santarem; one female Mararú, April. The Mararú paralectotype is labelled as type by Bequaert.

    Three additional paralectotypes (two females, Santarem; one female, Mararú) in the CMNH were described as "Var. (?)" and labelled as *E. foxi* Schulz by van der Vecht. One of the Santarem specimens lacks the head. Giordani Soika (1978:181) regarded these specimens as conspecific with *O. globicolle,* stating that *O. foxi* is a different species. It is evidently true that these specimens are not *foxi* Schulz, but we do not agree that they are conspecific with *globicolle.* The distinguishing characters used in Giordani Soika's (1978:59) key conflict: while these specimens match *globicolle* in the clypeus, the form of the parategula matches *foxi.* The pronotum with medially sparse punctation, a character not mentioned by Giordani Soika, also matches *foxi.* The "Var. (?)" of Fox appears to represent an undescribed species. The Santarem paralectotype of *cribrosa* also belongs to this species, not *globicolle.*
26. *Eumenes globicollis* Spinola; Fox, 1899:452, recorded from three specimens. Present are one female, Mararú, April; two females, Santarem; =*Omicron ypsilon* Giordani Soika, misidentification (according to Giordani Soika, 1978: 181).
27. *Eumenes gracilis* Fox, 1899:452, described from two specimens, Santarem. Junior homonym of *Eumenes gracilis* Saussure, 1852, =*Eumenes critica* Schulz (1906:214, new name) =*Omicron criticum* (Schulz). Lectotype female, Santarem, CMNH, designated by Giordani Soika (1978:120). The lectotype is missing the terminal segments of the metasoma. In the CMNH there is also one male, Santarem (paralectotype). Apparently Fox mistook the male for a female, for he mentioned having two specimens, but described only the female. The male is labelled by Bequaert as type. Giordani Soika's lectotype designation was inadvertent, when he referred to the female as "olotipo", mentioning that it had been labelled "holotype" by van der Vecht. We have appropriately labelled each specimen.

    Giordani Soika (1978) recognized four subspecies of *criticum.* These "subspecies" are distinguished in the key and descriptions solely by color, and we regard their recognition on that basis alone as without value. However, examination of the specimens in the MCZ reveals pronounced differences in the metanotal punctation, and to some extent in the clypeus, which are uncorrelated with the color differences. Giordani Soika (1978:123) described the metanotal punctation as "piccoli e radi", but most of the Brazilian specimens have medium punctation. The status of these forms should be reexamined.

28. *Eumenes fornicata* Fox, 1899:452, described from two males, Santarem, November, =*Minixi brasilianum* (Saussure) (synonymy by Giordani Soika, 1978: 370). Lectotype male, Santarem, November, CMNH, by present designation. The paralectotype is also in the CMNH, labelled by Bequaert as type.
29. *Eumenes deforma* Fox, 1899:453, described from three specimens, Corumbá, April, =*Pirhosigma deforme* (Fox) (generic placement by Giordani Soika, 1978:230, 231). Lectotype female, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes one female and one male (paralectotypes). Fox described only the female.
30. *Eumenes pilosa* Fox, 1899:454, described from two specimens, "Rio de Janeiro and Chapada, November", =*Pirhosigma pilosum* (Fox), new combination. Lectotype female, Chapada, November, designated by Giordani Soika (1978:257). Additional material in the CMNH includes one female, Rio de Janeiro, November (paralectotype). The paralectotype is badly damaged by dermestids. Giordani Soika's lectotype designation was inadvertent, when he referred to the Chapada female as "lecto-olotipo". We have appropriately labelled each specimen.

Giordani Soika (1978:10, 254) established the monotypic genus *Tricomenes* for *E. pilosa* Fox. The only character by which it was differentiated from *Pirhosigma* in the key, a broad longitudinal median carina on the propodeum, is an autapomorphy of *pilosa*. Giordani Soika's discussion compared *Tricomenes* only to *Omicron*, but *pilosa* is clearly more closely related to *Pirhosigma*. It shares with the species in that genus the apomorphic form of the first metasomal tergum: apically flask-shaped, with a preapical fossa and the apical lamella not preceded by a transverse swelling, and the stem laterally with two longitudinal carinae. Giordani Soika (1978:230) characterized *superficiale* as having one carina, which is incorrect; the ventral carinae approximate medially. This petiole form is unique among members of the *Eumenes s. l.* clade (*cf.* Carpenter and Cumming, 1985). In addition, the pronotal carina is sinuous on the humeri, the parategula is thick and bluntly pointed, and the apical lamella of the second metasomal tergum is elongate, all of which are probably apomorphic conditions, although not unique. This also applies to the "inconsueto" [unusual] metasomal pilosity, mentioned by Giordani Soika (1978: 257). Further, *pilosa* may be closely related to two species described by Fox and now placed in *Pirhosigma, superficiale* and *deforme*. The second metasomal sternum is strongly depressed basally, followed by a noticeable swelling in all three species (actually, there is variation in *superficiale*, with some specimens of the subspecies *impurum* in the MCZ lacking a swelling). The female mandibular teeth are enlarged relative to the only other species of *Pirhosigma* available for comparison, *aenigmaticum* Giordani Soika (a probable synonym of *simulans* Saussure); this condition is exaggerated in *pilosa*. Unlike *superficiale* and *deforme*, the second metasomal tergum is not gibbous in *pilosa*.

Other distinguishing traits of *pilosa* are probably autapomorphies. Giordani Soika noted the presence of an incomplete pretegular carina (posterior to the spiracular operculum) and an epicnemial carina, which might be thought to be plesiomorphic (*cf.* Carpenter and Cumming, 1985). *Pirhosigma* is stated to have the pretegular carina absent or "molto confusamente accennata" and to lack an epicnemial carina (Giordani Soika, 1978:229). However, *deforme* does have an epicnemial carina ventrally, and *superficiale* has the pretegular carina similar to the condition in *pilosa,* only less pronounced. Actually, both character states may be secondary in *pilosa,* associated with its coarse punctation. The epicnemial carina is not really present dorsally in *pilosa,* rather the border between the impunctate anterior part and coarsely punctate posterior part of the episternum appears sharply differentiated. Other definite apomorphies include the forewing second recurrent vein (2m-cu) interstitial between the second and third submarginal cells (see Carpenter and Cumming, 1985). This is well known in the genus *Pararaphidoglossa,* but is also found in *Pirhosigma aenigmaticum.* The condition is approached in three female paratypes of *aenigmaticum* in the MCZ (from Costa Rica, Panama and Colombia), and is fully developed in two males in the MCZ, from Panama and Venezuela, labelled as paratypes by Giordani Soika but not listed in his description. Finally, the tegula of *pilosa* is much broader than in other species of *Pirhosigma,* but *aenigmaticum* approaches this state somewhat.

Recognition of *Tricomenes* thus renders *Pirhosigma* paraphyletic, and we herewith synonymize these genera, new synonymy. Both genera were described in 1978, with the detailed description of *Pirhosigma* appearing first. As first revisers, we select *Pirhosigma* as the valid name.

There is an additional specimen of *P. pilosum* in the MCZ, a female from Napo, Limoncocha, Ecuador, 250 m, 15–28 June 1976, S. and J. Peck.

31. *Eumenes tegularis* Fox, 1899:455, described from two specimens, Corumbá, March, and Chapada, April, =*Omicron tegulare* (Fox) (generic placement by Giordani Soika, 1978:60, 208). Lectotype female, Corumbá, March, CMNH, by present designation. In the CMNH is also one female, Chapada, April (paralectotype).
32. *Eumenes tuberculata* Fox, 1899:456, described from 24 females and one male, Corumbá, April and May, =*Omicron tuberculatum* (Fox) (generic placement by Giordani Soika, 1978:60, 203). Lectotype female, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes 18 females, Corumbá, April, one female and one male, May (paralectotypes). The latter two specimens are labelled by Bequaert as types. Fox described an unspecified number of females as "Var.(?)". In the collection are one female, Chapada, September, one female, January, one male without date; three females Mararú, April; which correspond to the description. The September female is labelled by Fox "*Eumenes tuberculata* ? var. ? Fox", however none of these localities was reported, and given the discrepancy in the number of specimens, it is perhaps questionable whether these are syntypes. In addition to having the petiole with the stem more slender, these specimens have the clypeus narrower than in typical *tuberculatum,* as in *aequale* Giordani Soika. These two species are distinguished in Giordani Soika's (1978:60) key primarily by clypeal proportions, as well as by the extent of reddish maculation on the mesosoma of *aequale.* The "Var.(?)" specimens are more extensively reddish than stated in the couplet for *aequale.* However, a paratype of *aequale jucundum* in the MCZ (a female from Trinidad, stated by Giordani Soika [1978] to be in the British Museum), has large reddish scutal and propodeal marks, contradicting the key. The coloration appears to be without much

value in distinguishing these species, hence the "Var.(?)" of Fox corresponds to *O. aequale jucundum.*

Giordani Soika (1978) described three subspecies of *aequale.* As with *Zeta argillaceum* (Carpenter, 1988) and several species discussed above, these "subspecies" are based solely on color, and their distributions overlap. *Omicron aequale jucundum* was described from Mexico and Trinidad, the nominotypical form occurs only in Mexico, and *O. aequale nigritum* was described from specimens ranging from Brazil to Venezuela. Giordani Soika (1978: 202, 203) recorded some variation in color in his descriptions, and the specimens in the Fox collection show that the variation is extensive. We are therefore treating *O. a. nigritum* and *O. a. jucundum* as synonyms of *aequale,* new status.

33. *Eumenes chalicodomae* Saussure; Fox, 1899:457, recorded from ten specimens; present are six females and two males, Chapada, February–April; one female, Corumbá, April; one female, Santarem; =*Brachymenes dyscherus* (Saussure). The specific synonymy was established by Bequaert (1925*a*). Giordani Soika (1961:243) placed this species in his new genus *Brachymenes.*

    The usual narrow, pale yellow band at apex of the petiole is absent in one female and two males from Chapada; in these specimens the thorax is also more extensively black.
34. *Eumenes canaliculatus* (Olivier); Fox, 1899:457, "A large series", present are 11 females and 22 males, Chapada, January, March, October, December; four females and eight males, Corumbá, April; three females, Santarem; one female, Rio, November; one male, Uacarizal; =*Zeta argillaceum* (L.). The synonymy was established by van der Vecht (1959:128), Giordani Soika (1975), and Carpenter (1988).
35. *Eumenes filiformis* Saussure; Fox, 1899:457, one female, Santarem =*Eumenes* (*Zeteumenoides*) *filiformis,* revised status.

    Giordani Soika (1972:110) described the genus *Zeteumenoides* for *filiformis* (the type species), *E. rufomaculatus* Fox and *E. fulvomaculatus* Fox. Later, Giordani Soika (1978:17, 40) treated *Zeteumenoides* as a subgenus of *Eumenes,* and the originally-included species as subspecies of *versicolor* (*fulvomaculatus* as a synonym of the nominotypical form, following Giordani Soika, 1941:223). His key distinguished the subspecies only by coloration, and although he illustrated (Giordani Soika, 1978: figs. 35, 37, 39) some differences in the digitus of the male genitalia, he characterized these as not appreciable (Giordani Soika, 1978:40). He cited agreement with van der Vecht for this treatment, but also remarked that it was a "notevoli perplessità" that Cooper had collected *rufomaculatus* and *filiformis* in the same locality. He suggested that this fact merited ecological and biological investigation.

    In contrast to the subspecies discussed previously, these taxa do appear to be distinct. The ranges overlap to some extent, but the coloration does not intergrade. In addition, morphological differences exist. These differences are subtle, but they appear to be consistent in the specimens examined in the MCZ. Besides the digitus, the clypeus differs. In *filiformis* it is somewhat more elongate and narrower than in the other two taxa, and the punctation is coarser basally in both sexes. In *versicolor,* the clypeal punctation is more superficial than in *rufomaculatus,* which is thus intermediate between the other two taxa.

    Thus, these taxa can be consistently diagnosed. We here follow the modern trend (Nelson and Platnick, 1981; Nixon and Wheeler, 1990) of treating diagnostically distinct taxa as species. The status of these three taxa is therefore revised, and we raise them again to species rank.

36. *Eumenes rufomaculata* Fox, 1899:457, described from two specimens, "Pedra Branca and Corumbá, April", =*Eumenes* (*Zeteumenoides*) *rufomaculatus,* revised status. Lectotype female, Corumbá, April, CMNH, by present designation. In the CMNH is also one female, Pedra Branca, April (paralectotype). The paralectotype is labelled as "cotype" by Bequaert. Although Giordani Soika (1978:17, 41) regarded *rufomaculatus* as a subspecies of *E. versicolor,* as discussed above, we here treat this taxon as a species.
37. *Eumenes fulvomaculata* Fox, 1899:458, described from two females, Santarem, =*Eumenes* (*Zeteumenoides*) *versicolor* Saussure (synonymy by Giordani Soika, 1941:223). Lectotype female, Santarem, CMNH, by present designation. In the CMNH is also the paralectotype, labelled as "cotype" by Bequaert. Giordani Soika (1978:37, 41) referred to three types, evidently a *lapsus.* As discussed above and in contrast to Giordani Soika (1978), we here treat *versicolor* as a monotypic species.

In addition to these species, there is a series of specimens identified by Fox as *Eumenes infernalis* Saussure, however he did not include it in his publication. This species is represented by one female and three males, Chapada, December, and two males collected in January. This species is the type species of the genus *Cyphomenes* Giordani Soika. Giordani Soika (1978:222) included this series in his list of specimens examined.

Montezumia

1. *Montezumia sparsa* Fox, 1899:462, described from six females, Chapada, March. The MCZ contains a single female, labelled by Bequaert "*Montezumia sparsa* Fox paratype (like holotype)." This specimen is herewith designated as lectotype. This is evidently the specimen seen by Willink (1982:134). According to John E. Rawlins of the CMNH all the other specimens are lost. All the *Montezumia* and *Monobia* specimens studied by Fox were sent out on loan in 1974 by George Wallace separately from the other Eumeninae; they were intended to be studied by Abraham Willink through the intermediary of Karl V. Krombein at the U.S. National Museum of Natural History. There is no record of the loan ever arriving, and it evidently disappeared in the mail.

Monobia

1. *Monobia curvata* Fox, 1899:463, described from five females and two males, Chapada, March and November. Willink (1982:234) saw a female and male from the MCZ, and referred to the male as "paratipo". That male is no longer present in the MCZ, but the female, collected in March, is. This specimen is designated as lectotype, because the rest of the type series was apparently lost along with the *Montezumia* mentioned above.

Odynerus

1. *Odynerus* (*Stenancistrocerus*) *apicipennis* Fox, 1902:44, described from two females and three males, Chapada, March, December; Corumbá, April; =*Stenonartonia apicipennis* (Fox), new combination. Lectotype female, Chapada, March, CMNH, by present designation. Additional material in the

CMNH includes one male, Chapada, December; one male Corumbá, April (paralectotypes). In the MCZ is a male from Corumbá, April, labelled by Bequaert as "paratype", and a female from Chapada, March. These are evidently the other syntypes, and we have labelled them paralectotypes. There is a male in the CMNH from Pedra Branca, April, labelled "*Odynerus apicipennis* Fox type" in an unknown hand, but this locality was not mentioned by Fox.

Stenonartonia Giordani Soika, 1973, is a replacement name for *Paranortonia* Giordani Soika, 1941, a junior homonym of *Paranortonia* Bequaert, 1940. Originally included species are the type species *polybioides* (Schulthess), *lugens* (Schulthess), *mimica* (Kohl), *guaranitica* (Bertoni) and *flavotestacea* Giordani Soika. *Nortonia lugens* Schulthess, 1904, and *Odynerus paraguayensis* Brèthes, 1909, are junior synonyms of *apicipennis* (new synonymy). Giordani Soika (1941:154) stated that this genus is related to *Leptomenes,* an Afrotropical genus related to the "*Stenodynerus–Microdynerus* component" of Carpenter and Cumming (1985), but this appears to be incorrect. The form of the tegula and the pronotal punctation ally *Leptomenes* with *Stenodynerus,* whereas *Stenonartonia* seems to be part of the "*Pseudodynerus–Montezumia*" clade, sharing with these genera the synapomorphy of a slitlike axillary fossa (*cf.* Carpenter and Cumming, 1985). In terms of derived traits, *Stenonartonia* and *Leptomenes* superficially resemble one another only in having the propodeal valvula fused with the submarginal carina, but while the latter is pointed in *Leptomenes,* in *Stenonartonia* only *apicipennis* has this condition. The valvula is larger, and the carina more effaced in *Stenonartonia. Stenonartonia* is autapomorphic in having a transverse carina on metasomal tergum I, a trait that has evolved numerous times within Eumeninae (Carpenter and Cumming, 1985).

Additional specimens of *apicipennis* examined are as follows. BRAZIL: five females and ten males, Santa Catarina, Nova Teutonia, 1948, 1964–65 and 1967, F. Plaumann (MCZ; National Natuurhistorisch Museum, Leiden; University of California, Davis; Snow Entomological Museum, Lawrence); two males, Sâo Paulo, 29–31 January 1969, C. Porter (MCZ); one male, Uacarizal, February (MCZ). ARGENTINA: one female, Paso de la Patria, 5–7 November 1969; one female, Sombrerito, 8 November 1969; one female, Santa Anna, 8 May 1971, C. Porter and L. Stange (Instituto Miguel Lillo, Tucumán, one female now in Leiden); two males, Yuto, 10 January 1966, H. and M. Townes (American Entomological Institute and Leiden); two females, Salta, Rio Pescado, 19–25 November 1967; four females and ten males, Orán, Abra Grande, 18–25 December 1968 and 18 April–5 May 1969; one female, near Pocitos, 28 April 1968; three females, Tucumán, Horco Molle, 10–23 December 1962, 25 March–30 April 1966, 9–30 April 1968; one female, near Tafí del Valle, 5 April 1968; one female, Va. Padre Monte–R. Nio, 25 April 1966; all C. Porter (MCZ). BOLIVIA: one female, Coroico (University of California, Davis); one male, 24 km W of Coripata, June 1969, P. and P. Spangler (U.S. National Museum of Natural History). PARAGUAY: one male, Villarrica, August 1940, F. H. Schade (U.S. National Museum of Natural History); same locality, three females and three males (one male determined as *lugens* by Bequaert) MCZ.

The punctation of the clypeus and first and second metasomal terga appears to be variable, particularly in the males. For example, in the males from

Pedra Branca and Paraguay the punctation of the posterior part of tergum II is much denser and coarser than in the other males listed above.

2. *Odynerus* (*Stenancistrocerus*) *convolutus* Fox, 1902:45, described from two females and seven males from Corumbá, April, =*Stenodynerus convolutus* (Fox), new combination. Lectotype female, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes one female and seven males (paralectotypes). In the MCZ is an additional male with the same locality and date labels, and labelled by Bequaert a "paratype" of this species. It is possible that Fox miscounted, but there must remain some doubt about whether this specimen was part of the syntype series. We have nevertheless labelled the specimen as paralectotype.
3. *Odynerus* (*Stenancistrocerus*) *suffusus* Fox, 1902:46, described from eight specimens, "Corumbá and Pedra Branca, April", =*Stenodynerus suffusus* (Fox), new combination. Lectotype male, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes five males, Corumbá, April; one male Pedra Branca, April (paralectotypes). In the MCZ are one female and one male labelled as "paratype" by Bequaert. The male is from Corumbá, April, and is evidently the remaining syntype (paralectotype). The female, which is labelled only "highland, April", is actually *Cephalastor rufosuffusus* (species no. 20), *q.v.*, and was evidently labelled incorrectly by Bequaert.

   An unidentified female in the CMNH, labelled "Chapada, Nov." appears to belong to this species.
4. *Odynerus* (*Stenancistrocerus*) *areatus* Fox, 1902:47, described from two specimens, Chapada, March and December, =*Parancistrocerus areatus* (Fox), new combination. Lectotype male, Chapada, December, CMNH, by present designation. The CMNH also has one male, Chapada, March (paralectotype).
5. *Odynerus abdominalis* Fox, 1902:48, described from three specimens, Chapada, March and December, =*Hypancistrocerus abdominalis* (Fox), new combination. The CMNH also has a female from Chapada, March (paralectotype). A female from Chapada, December, in the MCZ, labelled by Bequaert "paratype", is evidently the remaining syntype (paralectotype).
6. *Odynerus* (*Stenancistrocerus*) *dentiformis* Fox, 1902:48, described from seven females and nine males, Corumbá, April; Chapada, December; =*Hypancistrocerus dentiformis* (Fox), new combination. Lectotype female, Corumbá, April, CMNH, by present designation. Additional material in the CMNH includes three females and eight males, Corumbá, April; one female, Chapada, December (paralectotypes). In the CMNH is also a female labelled only "Brazil" that was perhaps a syntype (paralectotype). In the MCZ are one female and one male from Corumbá, April, labelled by Bequaert as "paratype", which are evidently from the syntype series (paralectotypes).
7. *Odynerus* (*Ancistrocerus*) *fulvimaculus* Fox, 1902:49, described from two females, Chapada, April, =*Ancistroceroides fulvimaculus* (Fox), new combination. Lectotype female, Chapada, April, CMNH, by present designation. The CMNH also has the paralectotype.

   Ancistroceroides Saussure, 1855, is the generic name applicable to most of the Neotropical species that have been described in *Ancistrocerus*. Bequaert (1925*b*:61) designated *Odynerus cruentus* Saussure as type species, but since this proved to be a species of the very large Australian genus *Paralastor* Saussure, van der Vecht (1983:111) requested the International Commission on Zoological Nomenclature to reject Bequaert's designation and to designate *Odynerus alastoroides* Saussure as the type species. This was done in Opinion 1363 (International Commission on Zoological Nomenclature, 1985*b*).

8. *Odynerus* (*Ancistrocerus*) *rufimaculus* Fox, 1902:50, described from one female and three males, "Corumbá and Pedra Branca in April", =*Ancistroceroides rufimaculus* (Fox), new combination. Lectotype female, Corumbá, April CMNH, by present designation. Additional material in the CMNH includes one male, Corumbá, April; one male, Pedra Branca, April (paralectotypes). In the MCZ is a male from Corumbá, May, and labelled by Bequaert as "paratype", which may be the remaining syntype, although Fox did not give May as a date (paralectotype).
9. *Odynerus* (*Stenancistrocerus*) *atripes* Fox, 1902:51, described from 11 females and 27 males, Chapada, January, May, October; Corumbá, April; =*Ancistroceroides atripes* (Fox), new combination. Lectotype female, Chapada, January, CMNH, by present designation. Additional material in the CMNH includes five females and five males, Chapada, January, one female, May, 12 males, October, one female and three males, December, one female and four males without date; one male, Corumbá, April (paralectotypes). The December date was not mentioned by Fox, doubtless through oversight. Another female from Chapada, October, and a female labelled only "Jan.", are actually *Ancistroceroides conjunctus* (Fox), misidentification (paralectotypes). In the MCZ are a female from Chapada without date, and a male from Chapada, October, both labelled as "paratype" by Bequaert (paralectotypes).
10. *Odynerus* (*Ancistrocerus*?) *conjunctus* Fox, 1902:52, described from "Three females, numerous males", Chapada, April, September, October, December; Corumbá, April; =*Ancistroceroides conjunctus* (Fox), new combination. Lectotype female, Chapada, September, CMNH, by present designation. Additional material in the CMNH includes one female and two males, Chapada, September, one female and ten males, October, two males, November, one male, December, one male, May, four males, without date; one female and 14 males, Corumbá, April, one male, without date; four males without labels (paralectotypes). Another two males from Chapada, October, are actually *Ancistroceroides cordatus* (Fox), misidentification. In the MCZ is another male from Chapada, September, labelled by Bequaert as "paratype" (paralectotype).

    Here also belong one female from Chapada, October, and one female labelled only "Jan.", which were part of the syntype series of *Odynerus atripes* Fox.
11. *Odynerus* (*Hypancistrocerus*) *advena* Saussure, Fox, 1902:53, recorded from a "large series" from Corumbá and Chapada. Present are five females and 31 females, Corumbá, April, one male, May, one male, February, one male, without date, =*Hypancistrocerus advena* (Saussure). There is also one male, Mararú, April, a locality not mentioned by Fox. In the MCZ is another male from Corumbá, April, labelled by Bequaert as "*Ancistrocerus advena* Sss. named by Fox", which was evidently part of this series.

    The yellow spot in front of the scutellum is absent in three males from Corumbá and in the male from Mararú. The specimen recorded by Fox from Chapada appears to belong to a different species, however, its metasoma is lacking.
12. *Odynerus* (*Hypancistrocerus*) *reflexus* Fox, 1902:53, described from an un-

specified number of specimens from Chapada, December, January, May; and Corumbá, April. Junior homonym of *Odynerus reflexus* Brullé, 1839; =*Odynerus reflectorius* Dalla Torre, 1904:53, new name, =*Hypancistrocerus reflectorius* (Dalla Torre), new combination. Lectotype female, Chapada, September, CMNH, by present designation. Paralectotypes in the CMNH include two males, Chapada, January, one male, April, one male, May, seven males, December; one male, Corumbá, April. Fox did not mention the September and April dates for Chapada. However, the specimen we have designated as lectotype bears Fox's type label, so there seems to be little reason to doubt that these dates were overlooked. In the MCZ is another male from Chapada, January, labelled by Bequaert as "paratype" (paralectotype).

13. *Odynerus coxalis* Fox, 1902:54, described from two females and one male, Chapada, September; Corumbá, February; =*Hypancistrocerus coxalis* (Fox), new combination. Lectotype female, Chapada, September, by present designation. Additional material in the CMNH includes one male, Corumbá, February; one female, "Brazil" (paralectotypes).
14. *Odynerus herbertii* Fox, 1902:56, described from one female and 11 males, Chapada, September, December, January; Corumbá, April; =*Parancistrocerus herbertii* (Fox), new combination. Lectotype female, Chapada, December, CMNH, by present designation. Additional material in the CMNH includes one male, Chapada, January, one male, September; six males, Corumbá, April; one male without locality, April (paralectotypes). In the MCZ is another male from Corumbá, April, labelled by Bequaert as "paratype", which is evidently one of the missing syntypes (paralectotype).
15. *Odynerus cordatus* Fox, 1902:57, one female without locality label (holotype), =*Ancistroceroides cordatus* (Fox), new combination.

    Here also belong two males from Chapada, October, which were part of the syntype series of *Odynerus conjunctus* Fox. In addition to these specimens, the CMNH contains two males unidentified by Fox from Chapada, October and May, which belong to this species.
16. *Odynerus dorsonotatus* Fox, 1902:58, described from four specimens, Chapada, December, =*Parancistrocerus dorsonotatus* (Fox), new combination. Lectotype female, Chapada, December, CMNH, by present designation. The CMNH contains one additional female paralectotype, which is missing the terminal metasomal segments.
17. *Odynerus longicornis* Fox, 1902:59, one male Corumbá, April (holotype). Junior homonym of *Odynerus longicornis* Morawitz, 1895; =*Odynerus longicornutus* Dalla Torre, 1904:48, new name, =*Parancistrocerus longicornutus* (Dalla Torre), new combination.
18. *Odynerus striatus* Fox, 1902:60, described from three females and four males, Chapada, September, December, January, March, =*Parancistrocerus striatus* (Fox), new combination. Lectotype female, Chapada, September, CMNH, by present designation. Additional material in the CMNH includes one female and two males, Chapada, December, one female and two males, January, one male, March (paralectotypes). Fox recorded only seven specimens, but there is nothing to indicate that any of the specimens present do not belong, so we are inferring that he miscounted. In the MCZ is another male from Chapada, March, labelled by Bequaert as "paratype", which may also be a syntype (paralectotype).

    In addition to the specimens noted above, the CMNH contains eight males unidentified by Fox from Chapada, collected from October to January, which belong to this species.

19. *Odynerus inusitatus* Fox, 1902:61, described from two males, Chapada, December, =*Hypancistrocerus inusitatus* (Fox), new combination. Lectotype male, Chapada, December, by present designation. The CMNH also contains the paralectotype male.
20. *Odynerus rufosuffusus* Fox, 1902:62, described from three females, Corumbá, April, =*Cephalastor rufosuffusus* (Fox), new combination. Lectotype female, Corumbá, April, CMNH, by present designation. The CMNH also contains a paralectotype. In the MCZ is a female, which is labelled only "highland, April", and "*Ancistrocerus suffusus* Fox paratype" by Bequaert. This is evidently the remaining syntype, with Bequaert's label being an error (paralectotype). The CMNH paralectotype belongs to the "Var. b" described by Fox.

    Cephalastor Giordani Soika (1982:33, 40) was described as a monotypic subgenus of *Hypalastoroides*. Carpenter (1986:67) synonymized the type species, *H. depressus* Giordani Soika, 1969, with *Odynerus relativus* Fox, 1902. *Cephalastor* is not closely related to *Hypalastoroides*; it does not possess the outstanding apomorphy of the latter genus. Figure 2 in Giordani Soika (1969), showing a clearly petiolate second submarginal cell in the forewing of *depressus,* is inaccurate. On the type specimen, the cell is petiolate only on one wing; it is strongly narrowed on the other. Nor is the cell basally truncate, as in *Hypalastoroides* and closely related genera, rather it is acute. Carpenter (1986) raised *Cephalastor* to generic rank: it is part of the "*Stenodynerus–Leucodynerus* component" of Carpenter and Cumming (1985), sharing with members of that clade an expanded, campanulate tegula.
21. *Odynerus relativus* Fox, 1902:63, one female Corumbá, April (holotype), =*Cephalastor relativus* (Fox) (generic placement by Carpenter, 1986:67).
22. *Odynerus praecox* Saussure; Fox, 1902:63, recorded from "Eight females, and a large series of males". Present are one female, Chapada, March, one female, April, nine males, September, two females and nine males, October, 12 males, November; one male, Corumbá, February, two females and 18 males, April; two females and three males, Santarem; one female and one male, Uacarizal, February; one male, Mararú, April; one female and three males, Pedra Branca; =*Pachodynerus praecox* (Saussure). The Uacarizal and Mararú localities were not mentioned by Fox. In the MCZ are a female from Chapada without date, labelled by Bequaert "*Od. praecox* Sss. named by Fox", and a male from Chapada, November, which apparently belonged to this series.

    In most specimens only metasomal terga I and II have a yellow band; in one of the females from Santarem and in the males from Pedra Branca, tergum III is also banded; another female and the males from Santarem have bands on terga I–V or I–VI, respectively.

    Two additional males from Corumbá, April, appear to represent an undescribed species. The clypeus has macropunctures and is not closely micropunctate, there is no mesopleural process, and metasomal tergum I is unbanded. There is some variation in *praecox* in the degree of development of the mesopleural process and band on tergum I, but the clypeus of these specimens is quite different from that of all *praecox* we have examined.
23. *Odynerus nasidens* Latreille; Fox, 1902:63, one female Chapada, September, =*Pachyodynerus nasidens* (Latreille).
24. *Odynerus brevithorax* Saussure; Fox, 1902:63, one female, Chapada, April.

Not found. There is another female from Chapada, March, determined by Fox as "*Odynerus brevithorax* ? Sauss.", =*Pachodynerus brachygaster* (Saussure).

25. *Odynerus corumbae* Fox, 1902:63, one female, Corumbá, April (holotype), =*Pachodynerus corumbae* (Fox), new combination.
26. *Odynerus* (*Odynerus*) *chapadae* Fox, 1902:64, described from two females, Chapada, February and October, =*Pachodynerus argentinus* (Saussure) (synonymy by Willink, 1972:69). Lectotype female, Chapada, February, CMNH, by present designation. In the CMNH is also one female, Chapada, October (paralectotype). Willink (1972) mentioned seeing a specimen "from the original series of Chapada, in Harvard". Actually that specimen is only topotypical.
27. *Odynerus* (*Odynerus*) *sericeus* Fox, 1902:65, one female, Chapada, March (holotype), =*Pachodynerus sericeus* (Fox), new combination.
28. *Odynerus* (*Stenodynerus*) *serratus* Fox, 1902:65, one male Corumbá, April (holotype), =*Pseudodynerus serratus* (Fox) (generic placement by Bequaert, 1941:2, 6).
29. *Odynerus* (*Stenodynerus*) *griseus* Fox, 1902:66, described from two females and two males, Chapada, March; Corumbá, April; = *Pseudodynerus griseus* (Fox), revised status. Lectotype female, Chapada, March, CMNH, by present designation. In the MCZ are one female and one male from Chapada, March, labelled by Bequaert as "paratype", which are evidently the "paratypes" he mentioned in 1941 (paralectotypes). The Corumbá, April, specimen cannot be found.

    Bequaert (1941:6, 7) treated this taxon as a variety of *serratus*, stating that he was "unable to find a reliable structural character to separate" *griseus* and *serratus*. However, these taxa co-occur without intergrading in color. Not only were both described from Corumbá in the same month, in the MCZ are series of each collected at Nova Teutonia, Santa Catarina, with some specimens taken on the same dates. And although like Bequaert we have not found any diagnostic characters of external sculpturing that do not vary, dissections of the male genitalia reveal consistent differences. The digitus in *griseus* is somewhat more robust, and much more strongly haired. We therefore are treating *griseus* as a valid species.
30. *Odynerus* (*Stenodynerus*) *subapicalis* Fox, 1902:67, described from six females and one male; "Mararú and Chapada (April)"; Rio de Janeiro, November; Santarem; =*Pseudodynerus subapicalis* (Fox) (generic placement by Bequaert, 1941:2, 6). Lectotype female, Santarem, CMNH, by present designation. Additional material in the CMNH includes one female, Mararú, April; one female, Rio de Janeiro, November; two females, Chapada, April (paralectotypes).

ACKNOWLEDGMENTS

We thank John E. Rawlins of The Carnegie Museum of Natural History for his cooperation in the completion of this study, and Antonio Giordani Soika, Karl V. Krombein, Arnold S. Menke and Abraham Willink for their assistance in tracing the history of the loaned material. We also thank an anonymous reviewer with handwriting amazingly like Arnold Menke's for bringing the Papavero reference to our attention. Support for visits to Putten by the senior author was provided by a Milton Fund grant and National Science Foundation grant BSR-8508055; a visit to the Carnegie Museum was supported by National Science Foundation grant BSR-8817608.

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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 3, Pp. 243–251 4 September 1991

NEW SPECIES OF HYDROBIOSIDAE FROM ECUADOR (INSECTA: TRICHOPTERA: ANNULIPALPIA)

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Abstract

Twenty-five species of Hydrobiosidae (Trichoptera: Annulipalpia) are known from Ecuador. Six of these species are here described as new from streams in the Ecuadorian Andes: *Atopsyche davidsoni,* new species; *Atopsyche flinti,* new species; *Atopsyche milenae,* new species; *Atopsyche* (*Atopsaura*) *rawlinsi,* new species; *Atopsyche schmidi,* new species; *Atopsyche youngi,* new species. Two species previously known from Colombia, one species previously known from Peru and Bolivia, and one species widely distributed in Central and South America are recorded for the first time from Ecuador. New distributional information is given for five additional species of *Atopsyche,* and one species of *Cailloma.* A list of the Ecuadorian hydrobiosidae is given.

Introduction

The caddisfly fauna of higher elevations in South America is poorly known. In Ecuador, caddisflies of the family Hydrobiosidae have only been reported in the genera *Atopsyche* and *Cailloma* (Flint, 1974*b*; Harper and Turcotte, 1985). Species of *Atopsyche* are restricted to subtropical and tropical America ranging from south-central United States to Argentina. They are usually confined to higher elevations where the larvae live in cold, fast-flowing, often spring-fed streams.

Species of *Atopsyche* were revised by Ross and King (1952) and additional forms were described by Ross (1953). Since then, many species of *Atopsyche* have been discovered and described in various publications on Trichoptera from Central and South America (Flint, 1974*a*). However, the Ecuadorian caddisfly fauna has not been studied in detail. Harper and Turcotte (1985) described four new species of this genus collected during an ecological study of streams in the Ecuadorian Andes, mostly tributaries of the Río Matadero in the Quinuas Valley near Cuenca (altitude 3300 m). In a recent monograph on the family Hydrobiosidae, Schmid (1989) described 43 new species of *Atopsyche* from Central and South America, including ten new species from Ecuador. Five of these are discussed further in this paper.

The genus *Cailloma* has an interesting distribution, occurring in both Brazilian and Chilean subregions ranging from the eastern tip of Isla de Los Estados off the tip of Tierra del Fuego into Ecuador (Flint, 1974*b*).

Collections recently made by entomologists from the Carnegie Museum of Natural History in Pittsburgh include hydrobiosids from several remote, high elevation localities in Ecuador. These species, six of them undescribed, were collected in the Andes near rivers and streams at elevations ranging from 1080–3500 m. I describe here these six species of *Atopsyche* in the context of Schmid's revision, present additional locality records in Ecuador for previously described hydrobiosids, and provide a list of Hydrobiosidae currently known from Ecuador.

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Submitted 26 November 1990.

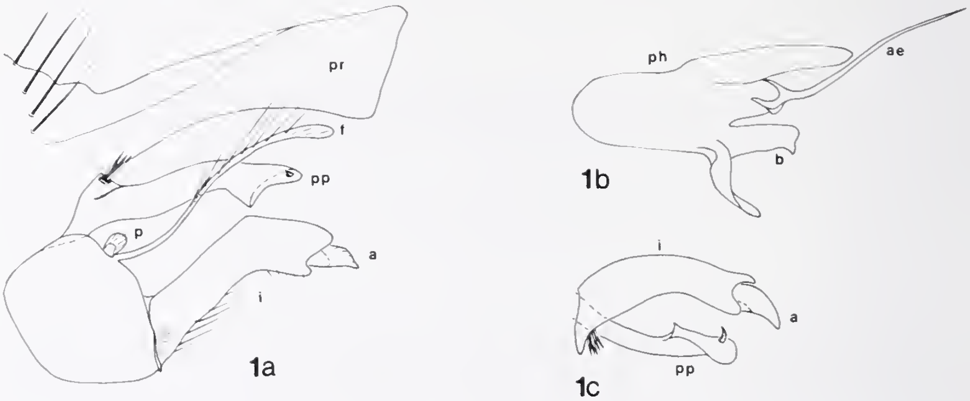

Fig. 1.—Male genitalia of *Atopsyche flinti,* new species: 1a, left lateral view; 1b, phallic apparatus, left lateral view; 1c, left inferior appendage and parapod, ventral view. Abbreviations: a, apical segment of inferior appendage; ae, aedeagus; b, beak of phallotheca; i, inferior appendage; f, filipod; p, preanal appendage; ph, phallotheca; pp, parapod; pr, proctiger.

Morphological terminology of genitalia generally follows that of Schmid (1989). Holotypes and most paratypes are deposited in the Carnegie Museum of Natural History (CMNH), Pittsburgh. One paratype each of *Atopsyche youngi, A. schmidi* and *A. milenae* are deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Atopsyche flinti, new species
(Fig. 1a–c)

Diagnosis.—Distinguished by the angled basal segment of inferior appendage, dilated caudal section of parapods armed with a prominent spine and phallic apparatus with unique rod-shaped aedeagus. The placement of this species within the genus is uncertain.

Description.—Male: Length of forewing 10 mm. Body dark brown; legs, palpi, and antennae brown; forewing membrane brown with dark hair. Fifth sternum of male abdomen with anterolateral process slightly longer than sternum. Posteromesal processes on sixth and seventh sterna absent. *Male genitalia* (Fig. 1): Parapods (Fig. 1a, c) each sausage-shaped, bent ventrad, with apex dilated, trumpet-shaped, bearing dorsoapical point located laterally and with three long spines on dorsobasal section. Filipods (Fig. 1a) as long as parapods, narrow and sigmoid; preanal appendages pear-shaped. Basal segment of inferior appendage (Fig. 1a, c) long and narrow, angled about 50% two-thirds distance from base with short ventral lobe and tuft of setae basomesally; apical segment very short and triangular, with pointed apex. Phallic apparatus (Fig. 1b) with basal section of phallotheca deep and inflated, with membranous dorsal lobe; aedeagus free, slightly sigmoid, with stylet-shaped rod as long as basal segment of inferior appendage; ventral section of phallic apparatus extended into pair of broad processes ("beaks of the phallotheca", Schmid, 1989), each with truncate apex bearing short ventral point.

Type specimen.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Chimborazo. 21 km ESE Licto, stream above Río Alao. 3500 m, 18–19 October 1987, R. Davidson, J. Rawlins, C. Young.

Atopsyche (Atopsaura) rawlinsi, new species
(Fig. 2a–c)

Diagnosis.—This species is in the *falina* group of Schmid (1989), related to *A. lobosa* Ross and *A. neolobosa* Flint. It differs from all other species by the shape

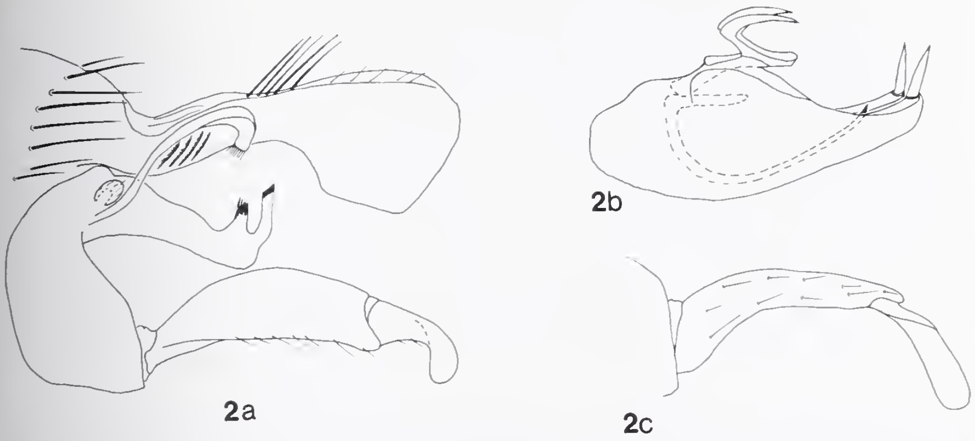

Fig. 2.—Male genitalia of *Atopsyche* (*Atopsaura*) *rawlinsi*, new species: 2a, left lateral view; 2b, phallic apparatus, left lateral view; 2c, left inferior appendage, ventral view.

of the parapods which bear two strong dorsoapical teeth, and the phallic apparatus with hook-like dorsal processes and two dorsoapical spines.

Description.—Male: Length of forewing 10 mm. Body brown; legs yellowish brown; antennae and palpi light brown; forewing membrane light brown with brown and golden hair. Fifth sternum with anterolateral processes reduced to short pocket-like structures; posteromesal process of sixth sternum slightly longer than sternum; that of seventh sternum about one-quarter length of sternum with basal section inflated. *Male genitalia* (Fig. 2): Parapods (Fig. 2a) with two strong, obliquely truncate dorsal teeth at apex; distal tooth elevated, longer than proximal. Filipods (Fig. 2a) half as long as proctiger, "C"-shaped; truncate apex pointed ventrad with brush of stiff short bristles at end. Preanal appendages small, button-shaped. Inferior appendage (Fig. 2a, c) with basal segment long, narrow at base, extending apically; apical segment finger-shaped, with rounded tip turned ventromesad. Phallic apparatus (Fig. 2b) broad at base with dorsal pair of strongly chitinized, "C"-shaped spines at midlength; beaks of phallotheca consisting of broad, fleshy lobes with rounded tips, each carrying a strong spine; aedeagus stylet-shaped with inner rod curved dorsad.

Type specimen.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Loja. Cordillera Cordoncillo, 11 km S Saraguro, 3130 m, 27 October 1987, R. Davidson, J. Rawlins and C. Young, cloud forest.

Atopsyche youngi, new species
(Fig. 3a–c)

Diagnosis.—This species is similar to *A. chirimachaya* Harper and Turcotte based on the short, rectangular inferior appendages and sausage-shaped parapods. It may be distinguished from all other species by the mesal expansion of the rectangular basal segment of each inferior appendage and by the tubular parapods each armed with an apicolateral projection. This and the following three species form a distinct group which is related to the *bicolorata* group of Schmid (1989), an assemblage not placed by him in an existing subgenus.

Description.—Male: Length of forewing 9–10 mm. Body brown; legs yellow; thorax covered with black hairs; forewing membrane brownish, slightly iridescent. Male abdomen with anterolateral processes of fifth sternum about as long as sternum, posteromesal process of sixth sternum about as long as sternum, that of seventh sternum very short. *Male genitalia* (Fig. 3): Parapods (Fig. 3a, c) sausage-shaped, deflected ventrad, similar to those of *bicolorata* group; apex of each parapod undivided, dilated in ventral aspect, curved mesad with lateral short spine located on apical third. Filipods (Fig. 3a) as long as parapods, subclavate; preanal appendages button-like. Basal segment of each inferior appendage

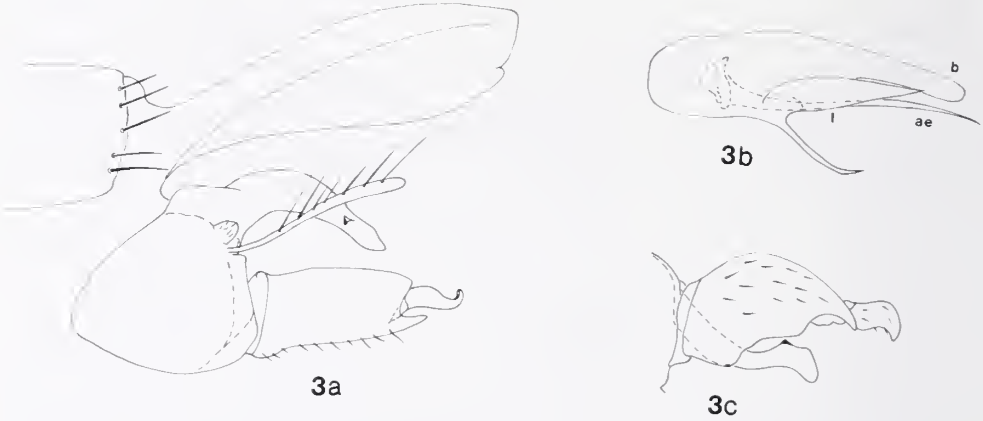

Fig. 3.—Male genitalia of *Atopsyche youngi,* new species: 3a, left lateral view; 3b, phallic apparatus, left lateral view; 3c, left inferior appendage and parapod, ventral view. Abbreviations: ae, aedeagus; b, beak of phallotheca; l, lateral extension of phallotheca.

(Fig. 3a, c) short, subrectangular, thick, with prominent ventroapical lobe; apical segment finger-like with apex curved dorsad. Phallic apparatus (Fig. 3b) with long stylet-shaped aedeagus, partially covered by beak of phallotheca bearing lanceolate, lateral extensions.

Type specimens.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Azuay. Pass 8 km NE Girón, 2600 m, 8 November 1987. J. Rawlins, C. Young, R. Davidson, montane woodland. Paratypes: 5 males, same data as holotype [4 paratypes (CMNH); 1 paratype (NMNH)].

***Atopsyche schmidi*, new species**
(Fig. 4a–c)

Diagnosis.—This species is similar to *A. yupanqui* Schmid but differs in the shape of the claspers and phallic apparatus. It is a member of the *bicolorata* group of Schmid (1989), unplaced as to subgenus. It can be distinguished from all known members of this group by the simple, sausage-shaped parapods, broad basal segment of inferior appendage with verrucose dorsoapical projection and the beak-shaped aedeagus.

Description.—*Male:* Length of forewing 9–10 mm. Body brown; legs and antennae yellowish brown; palpi dark brown; head and thorax with black hairs; forewing membrane iridescent brown with brownish hairs. Male abdomen with fifth anterolateral processes of sternum about as long as sternum; posteromesal process of sixth sternum about as long as sternum; that of seventh sternum about one-quarter length of sternum. *Male genitalia* (Fig. 4): Parapods (Fig. 4a) simple, lateral aspect of sausage-shaped apex deflected ventrad, without setae or teeth. Filipods (Fig. 4a) slender, as long as parapods, gradually clavate apically; preanal appendages button-like. Each inferior appendage (Fig. 4a, c) short; basal segment ovoid, with long, hooked ventroapical lobe, and with semitransparent, button-shaped, and verrucose dorsoapical structure; apical segment slightly longer than ventroapical lobe of basal segment, widened at base, constricted subapically. Phallic apparatus (Fig. 4b) with anterior section of phallotheca short, broad; beak-shaped aedeagus expanded dorsally in middle and lanceolate apically; paired lateral extensions of phallotheca short, blade-like, with pointed tips.

Type specimens.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Loja. Cordillera Cordoncillo, 11 km S Saraguro, 3130 m, 27 October 1987, R. Davidson, J. Rawlins and C. Young, cloud forest. Paratypes: 4 males, same data as holotype [3 paratypes (CMNH); 1 paratype (NMNH)].

***Atopsyche davidsoni*, new species**
(Fig. 5a–c)

Diagnosis.—This species seems to be closest to *A. chirimachaya* Harper and Turcotte, differing in the shape and inner structure of the inferior appendage and

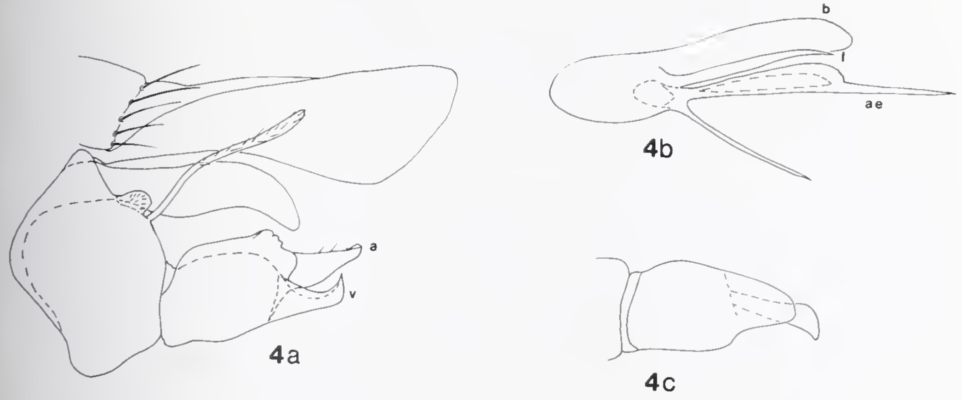

Fig. 4.—Male genitalia of *Atopsyche schmidi,* new species: 4a, left lateral view; 4b, phallic apparatus, left lateral view; 4c, left inferior appendage, ventral view. Abbreviations: a, apical segment of inferior appendage; ae, aedeagus; b, beak of phallotheca; l, lateral extension of phallotheca; v, ventroapical lobe of basal segment—inferior appendage.

in the length of posteromesal processes on the sixth and seventh sternum. It is a member of the *bicolorata* group of Schmid (1989). It differs from all other species by the shape and inner structure of inferior appendages with two strong projections on the mesal margin.

Description.—Male: Length of forewing 12 mm. Head and thorax dark brown with black hairs; legs yellowish brown; antennae brown with yellow rings at each segment; palpi brown; forewing membrane brownish grey, with brown hairs; small silver-grey spots at end of each vein on forewing apex, one or two spots in costal region. Abdominal segments devoid of pocket-like structures; fifth sternum with anterolateral processes about as long as sternum; posteromesal process of sixth sternum about three-quarters as long as sternum; that of seventh sternum one-third as long as sternum. *Male genitalia* (Fig. 5): Paired parapods (Fig. 5a) simple, sausage-shaped with apex divided into two shallow lobes, curved ventrad. Filipods (Fig. 5a) longer than parapods, slightly clavate apically; preanal appendages button-shaped. Each inferior appendage (Fig. 5a, c) short, robust with basal segment quadrangular from lateral aspect; ventral aspect extended mesad in center, bearing sharp point directed dorsad, with sickle-

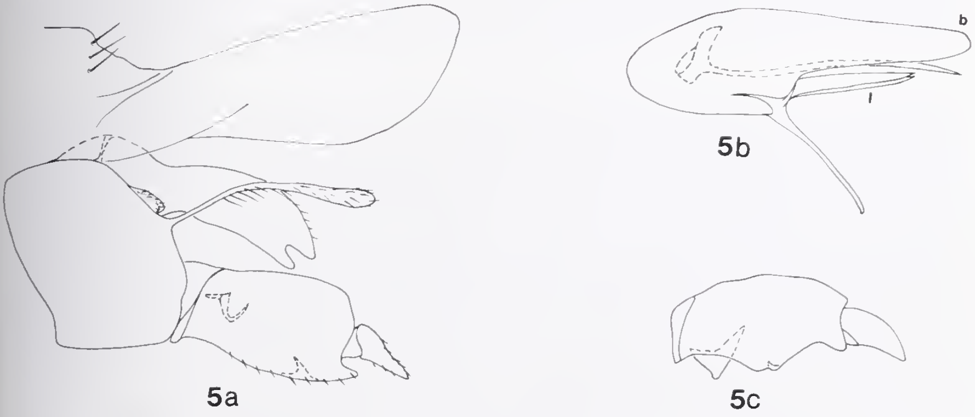

Fig. 5.—Male genitalia of *Atopsyche davidsoni,* new species: 5a, left lateral view; 5b, phallic apparatus, left lateral view; 5c, left inferior appendage, ventral view. Abbreviations: b, beak of phallotheca; l, lateral extension of phallotheca.

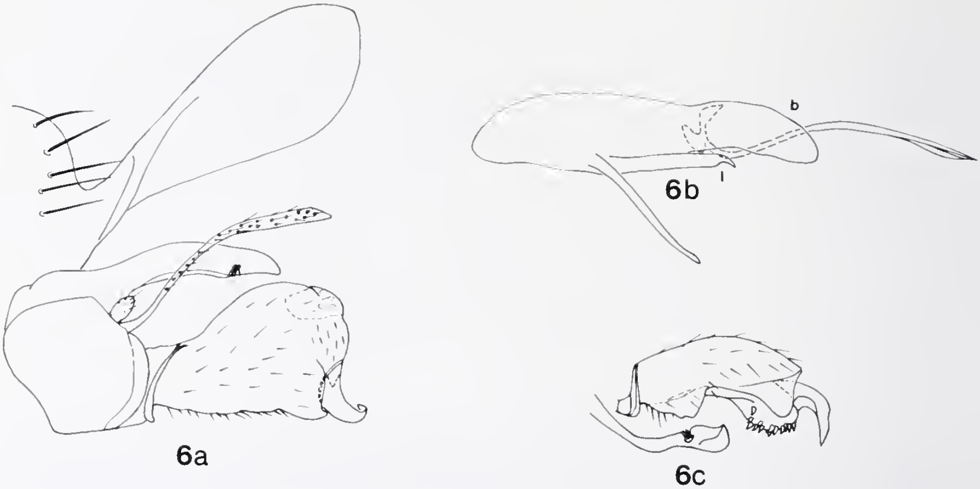

Fig. 6.—Male genitalia of *Atopsyche milenae,* new species: 6a, left lateral view; 6b, phallic apparatus, left lateral view; 6c, left inferior appendage and parapod, ventral view. Abbreviations: b, beak of phallotheca; l, lateral extension of phallotheca.

shaped crest on basomesal section; apical segment short, triangular, with pointed tip curved mesad. Phallic apparatus (Fig. 5b) similar to *A. schmidi* with dorsobasal section of phallotheca transparent, inflated; lateral extensions of phallotheca lanceolate, with pointed tips; aedeagus is a narrow central rod.

Type specimen.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Bolívar. 16 km NNE Guaranda, 3420 m, 16 October 1987. R. Davidson, J. Rawlins, C. Young, grassland.

Atopsyche milenae, new species
(Fig. 6a–c)

Diagnosis.—Distinguished by the short, broad and triangular inferior appendage with spines on the dorsomesal surface; long, rod-shaped aedeagus, and hooked lateral extensions of phallotheca. It is a member of the *bicolorata* group, differing from the other members of the group in the shape and inner structure of the male genitalia.

Description.—*Male:* Length of forewing 14 mm. Body color brown; antennae and palpi brown; legs yellowish; forewing membrane smoky brown, covered with blackish hair. Anteromesal processes on fifth sternum little longer than segment, with hooked apex; posteromesal process on seventh sternite very short, knob-like; that of sixth sternum absent. *Male genitalia* (Fig. 6): Lateral aspect of parapods (Fig. 6a) curved slightly ventrad with group of short spines on posteromesal surface. Filipods (Fig. 6a) slightly clavate, as long as basal segment of inferior appendage; preanal appendages oval. Basal segment of each inferior appendage (Fig. 6a, c) triangular, large, robust, rounded at apex, with prominent, rounded, ventroapical lobe curved mesad; rectangular area on dorsomesal surface of basal segment of inferior appendage covered with short, thick spines; finger-like apical segment with blunt tip curved mesad. Phallic apparatus (Fig. 6b) with broad phallothecal base and narrow apical section; aedeagus with long stylet-like rod extending far beyond membranous beak of phallotheca; lateral extensions of phallotheca short, stout, with hooked apices.

Type specimens.—Holotype, male (CMNH). *Verbatim label data:* ECUADOR: Bolívar. 16 km NNE Guaranda, 3420 m, 16 October 1987. R. Davidson, J. Rawlins, C. Young, grassland. Paratype: 1 male paratype (NMNH), same data as holotype.

NOTES ON DISTRIBUTION OF PREVIOUSLY DESCRIBED SPECIES

***Atopsyche banksi* Ross**. ECUADOR: Chimborazo. 11 km NE Pallatanga. 2800 m, 11 November 1987. C. Young, R. Davidson, J. Rawlins, semiarid environment; 1 male. NEW RECORD FOR ECUADOR, previously known from Colombia (Ross, 1953).

***Atopsyche callosa* Navas**. ECUADOR: Loja. 45 km SSE Portovelo, Río Yaguachi, 1080 m, 4 November 1987, R. Davidson, J. Rawlins and C. Young, riparian scrub; 2 males. Zamora-Chinchipe. 8 km NW Zamora, mouth of Río Sabanilla, 1420 m, 11 November 1987, J. Rawlins, R. Davidson, C. Young; 1 male. Azuay. Río León, 6 km N Oña, 1860 m, 16 October 1987, J. Rawlins, C. Young, R. Davidson, xeric desert at river; 2 males. NEW RECORDS FOR ECUADOR, previously known from Costa Rica, Panama, Venezuela, Colombia, and Peru (Flint, 1975).

***Atopsyche clarkei* Flint**. ECUADOR: Morona-Santiago. Río Culebrillas, 34 SE Gualacéo, 2200 m, 22–23 October 1987, J. Rawlins, R. Davidson, C. Young, wet forest; 1 male. NEW RECORD FOR ECUADOR, previously known from Colombia (Flint, 1963).

***Atopsyche copayapu* Schmid**. ECUADOR: Loja. 45 km SSE Portovelo, Río Yaguachi, 1080 m, 4 November 1987, R. Davidson, J. Rawlins and C. Young, riparian scrub; 2 males. Previously known from both sexes at the type locality: Ecuador, Pichincha, 14 km E Santo Domingo de los Colorados (Schmid, 1989).

***Atopsyche incatupac* Schmid**. ECUADOR: El Oro. 9 km NW Atahualpa, 1860 m, 5 November 1987, J. Rawlins, C. Young, R. Davidson, cloud forest; 4 males. Previously known from both sexes at the type locality: Ecuador, Cotopaxi, 113 km W Latacunga, 4500 ft (Schmid, 1989).

***Atopsyche neolobosa* Flint**. ECUADOR: Loja. Cordillera Cordoncillo, 11 km S Saraguro, 3130 m, 27 October 1987, R. Davidson, J. Rawlins and C. Young, cloud forest; 1 male. Previously known from both sexes at the type locality: Ecuador, Napo, Papallacta, 10,500 ft (Flint, 1963).

***Atopsyche pachacutec* Schmid**. ECUADOR: El Oro. 9 km NW Atahualpa, 1860 m, 5 November 1987, J. Rawlins, C. Young, R. Davidson, cloud forest; 1 male. Previously known from both sexes at the type locality: Ecuador, Cotopaxi, 113 km W Latacunga, 4500 ft (Schmid, 1989).

***Atopsyche puharcocha* Schmid**. ECUADOR: Morona-Santiago. Río Culebrillas, 34 km SE Gualacéo, 2200 m, 22–23 October 1987, J. Rawlins, R. Davidson, C. Young, wet forest; 1 male. NEW RECORD FOR ECUADOR. O. S. Flint compared this Ecuadorian specimen of *A. puharcocha* with a series of the same species collected in Bolivia and Peru and deposited in the National Museum of Natural History. He observed that each geographic sample differs slightly from the others, but in no consistent manner, suggesting that the species is highly variable. The species is previously recorded from Bolivia (Cochabamba, La Paz) and Peru (Cuzco) (Schmid, 1989).

***Atopsyche tampurimac* Schmid**. ECUADOR: Zamora-Chinchipe. 8 km NW Zamora, mouth of Río Sabanilla, 1420 m, 11 Nov 1987, J. Rawlins, R. Davidson, C. Young; 1 male. Previously known only from the male holotype taken at San Francisco de Borja, Napo, Ecuador (Schmid, 1989).

***Cailloma lucidula* (Ulmer).** ECUADOR: Chimborazo. 21 km ESE Licto, stream above Río Alao, 3500 m, 18–19 October 1987, R. Davidson, J. Rawlins, C. Young; 1 male. Previously known from Ecuador (Flint, 1974*b*).

HYDROBIOSIDAE KNOWN FROM ECUADOR

Atopsyche (*Atopsyche*)

**Atopsyche* (*Atopsyche*) *banksi* Ross. ECUADOR: Chimborazo.
Atopsyche (*Atopsyche*) *catherinae* Harper and Turcotte. ECUADOR: Azuay.
Atopsyche (*Atopsyche*) *chirihuana* Schmid. ECUADOR: Pichincha.
**Atopsyche* (*Atopsyche*) *copayapu* Schmid. ECUADOR: Loja, Pichincha.
**Atopsyche* (*Atopsyche*) *incatupac* Schmid. ECUADOR: Cotopaxi, El Oro.
Atopsyche (*Atopsyche*) *janethae* Harper and Turcotte. ECUADOR: Azuay.
Atopsyche (*Atopsyche*) *maitacapac* Schmid. ECUADOR: Napo, Pastaza.
Atopsyche (*Atopsyche*) *mancocapac* Schmid. ECUADOR: Pastaza.
**Atopsyche* (*Atopsyche*) *pachacutec* Schmid. ECUADOR: Cotopaxi, El Oro.
**Atopsyche* (*Atopsyche*) *tampurimac* Schmid. ECUADOR: Napo, Zamora-Chinchipe.
Atopsyche (*Atopsyche*) *tlaloc* Schmid. ECUADOR: Azuay.

Atopsyche (*Atopsaura*)

**Atopsyche* (*Atopsaura*) *callosa* Navas. ECUADOR: Loja, Zamora-Chinchipe, Azuay.
**Atopsyche* (*Atopsaura*) *clarkei* Flint. ECUADOR: Morona-Santiago.
**Atopsyche* (*Atopsaura*) *neolobosa* Flint. ECUADOR: Loja, Napo.
**Atopsyche* (*Atopsaura*) *puharcocha* Schmid. ECUADOR: Morona-Santiago.
**Atopsyche* (*Atopsaura*) *rawlinsi,* new species. ECUADOR: Loja.
Atopsyche (*Atopsaura*) *sinchicurac* Schmid. ECUADOR: Zamora-Chinchipe.

Atopsyche (subgenus uncertain)

Atopsyche chirimachaya Harper and Turcotte. ECUADOR: Azuay.
Atopsyche cajas Harper and Turcotte. ECUADOR: Azuay.
**Atopsyche davidsoni,* new species. ECUADOR: Bolívar.
**Atopsyche flinti,* new species. ECUADOR: Chimborazo.
**Atopsyche milenae,* new species. ECUADOR: Bolívar.
**Atopsyche schmidi,* new species. ECUADOR: Loja.
**Atopsyche youngi,* new species. ECUADOR: Azuay.

Cailloma

**Cailloma lucidula* (Ulmer). ECUADOR: Chimborazo.

*Discussed in this paper.

ACKNOWLEDGMENTS

This study was made possible through the effort of J. E. Rawlins, C. W. Young and R. L. Davidson who collected the material described in this paper. J. E. Rawlins provided suggestions with respect to final manuscript preparation. P. Gavaghan reviewed the paper and provided technical support needed for specimen preparation. Mark A. Klingler reviewed the figures and corrected the final drawings.

The author also extends sincere thanks to Dr. Oliver S. Flint, Jr., Smithsonian Institution, Washington, D.C., and Dr. Fernand Schmid, Biosystematics Research Institute, Agriculture Canada, Ottawa, for their help in comparing specimens of new taxa with material available to them.

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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 3, Pp. 253–254 4 September 1991

REVIEWS

PHYTOGEOGRAPHY AND VEGETATION ECOLOGY OF CUBA. By A. Borhidi. 1991. Akadémiai Kiadó, Budapest. 858 p., 16 color plates, map in pocket. ISBN 963 05 5295 7.

Phytogeography and Vegetation Ecology of Cuba represents the culmination of more than 20 years of work on the vegetation and flora of Cuba by Attila Borhidi and his colleagues, particularly the Cuban botanists Julian Acuña Gale and O. Muñiz. Although there are many such detailed studies of temperate vegetation, this is one of a few major works of its kind on tropical plants. This book presents a classic descriptive plant ecology of Cuba based on years of field work. Those seeking more modern comparative analyses of plant communities will be disappointed. However, Borhidi's book lays an impressive groundwork for future studies in the American tropics.

Cuba is the largest Caribbean island with a total area, including offshore islands and reefs, of 110,922 km^2. Cuba also has the most diverse flora in the Caribbean with 6500 species of vascular plants and the highest percentage of endemic taxa (72 endemic genera and approximately 3200 endemic species) of any Caribbean island. Unlike studies of the vegetation ecology of temperate regions with well-known floras, a necessary component of this work was a taxonomic inventory along with extensive field surveys. In the course of this research, 20,000 plant specimens were collected, including five new genera and more than 350 new species and infraspecific taxa.

Cuba is also one of the most disturbed islands in the Caribbean. Borhidi states that more than 75 percent of the island is presently covered by secondary growth, agricultural fields, and other man-disturbed vegetation formations. As one of Borhidi's objectives was a modern reconstruction of the potential natural vegetation, the gathering and analysis of data on climate, soil, and other factors influencing vegetation formations were essential adjuncts to field surveys.

The result of this multi-faceted approach is a major compendium on the plants of Cuba, which includes data both on vegetation ecology and the underlying abiotic factors affecting plant growth. This book has brought together in one volume many of Borhidi's previous publications and expanded upon them.

In addition to introductory chapters on objectives and the methods used, the book is divided into five parts. Part I covers the "bioclimatological fundamentals" including the physical geography of Cuba, data on temperature and rainfall patterns, and a discussion of the relationships between climate and vegetation patterns.

Part II treats the more important aspects of the effects of soil on vegetation and contains a brief survey of Cuban soils. Distinctive soil types are discussed in separate chapters. Of particular interest are the large serpentine areas in Cuba, which cover only seven percent of the island, but which contain over 30 percent of the endemic taxa. The chapter in this section on the nature and origin of Cuban savannas clearly illustrates the author's focus on determining the *potential* natural vegetation rather than simply mapping the present Cuban vegetation. Many previous workers did not distinguish natural savannas from secondary savannas, and thus estimated that 25 to 50 percent of Cuba was originally covered by grasslands. In contrast, Borhidi concludes that when Columbus landed in Cuba, only two to three percent of the island was covered by natural savannas.

Part III deals with the fundamentals of Cuban phytogeography, including ecological aspects as well as the origin of the Cuba flora and its relationships with other Caribbean and neotropical floras. Borhidi presents a life-form analysis, modified for a tropical flora, which is based on 6375 taxa. Patterns of endemism and floristic distribution, both within Cuba and in relation to other floras, are discussed and mapped. These discussions are again presented in a classic descriptive format and do not include more recent methods for the analysis of historical biogeography.

The phytogeographical subdivisions of Cuba are outlined in Part IV, which acknowledges contributions by Muñiz. Three sub-provinces (western Cuba, central Cuba, and eastern Cuba), nine sectors, and 36 floristic districts are recognized based on geographical, geological, and soil conditions in addition to the flora and vegetation.

Part V presents the 37 main vegetation types of Cuba, which are based on physiognomic criteria rather than floristic composition. In addition to a discussion of each vegetation unit, there is a separate color-coded map (scale 1:1,250,000) of the potential natural vegetation of Cuba. The largest section is Part VI, a systematic review of the plant communities of Cuba. More than 150 phytosociological units (divided among 27 classes) are characterized. Data for woody plant communities relevant to both Parts V and VI are synthesized in a 149-page table as an appendix.

In summary, this is a data-rich book with copious illustrations, maps, and tables. There is little to criticize in its format. For the non-taxonomist, the addition of family names to the table in the appendix would be useful. The color photographs are poorly reproduced and the over-large type used for the names of taxon authors in the appendix is distracting. However, these and other minor problems do not detract from the overall quality of this work. Although criticisms can be made about the lack of more recent analytic methods and the absence of major synthesis, the reader can only be in awe of the amount of data presented in this book. *Phytogeography and Vegetation Ecology of Cuba* is an essential reference for anyone interested in tropical plant ecology.

SUE A. THOMPSON, *Collection Manager, Section of Botany.*

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ANNALS of CARNEGIE MUSEUM

THE CARNEGIE MUSEUM OF NATURAL HISTORY
4400 FORBES AVENUE • PITTSBURGH, PENNSYLVANIA 15213

VOLUME 60 27 NOVEMBER 1991 NUMBER 4

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Office of Scientific Publications
The Carnegie Museum of Natural History
4400 Forbes Avenue
Pittsburgh, PA 15213-4080
Phone (412) 622-3287
Fax (412) 622-8837

ANNALS OF CARNEGIE MUSEUM is published quarterly by The Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213-4080, by the authority of the Board of Trustees of Carnegie Institute.

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THE CARNEGIE
MUSEUM OF
NATURAL HISTORY

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.

ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 4, Pp. 255–319 27 November 1991

ARCHAEOLOGY OF FOUNTAIN CAVERN, ANGUILLA, WEST INDIES

David R. Watters
Associate Curator, Section of Anthropology

Abstract

Three test pits were excavated as part of an archaeological survey of Fountain Cavern, Anguilla, between 6–16 January 1986, with the assistance of the Anguilla Archaeological and Historical Society. Of 2493 artifacts, miscellaneous materials, and faunal remains recovered, 2037 (81.7%) were excavated from test pits. Archaeological remains were concentrated in Chamber 1, the front of the cavern, near 12 exceptionally well-preserved petroglyphs. Fountain Cavern is interpreted as a subterranean ceremonial center for the prehistoric peoples of Anguilla, making it a rare type site in the northern Lesser Antilles. Ceramics, mostly undecorated, are attributed to utilization of the cavern by post-Saladoid peoples, for ritual and perhaps water procurement activities, after ca. A.D. 600, and more specifically A.D. 900–1200, or later. Certain taphonomic processes, such as downward transport of historic and modern artifacts in test pit 1 where they intermingled with prehistoric artifacts, and active mixing of deposits in test pit 3 as the result of modern construction activities, as well as dubious radiocarbon dates, impose limits on interpretation of the archaeological remains. Nevertheless, the Fountain Cavern archaeological data support the conclusion that this site was an important post-Saladoid ceremonial center, an interpretation that is further supported by ethnohistorical evidence of the significance of caves for prehistoric peoples of the Caribbean islands.

Introduction

An archaeological survey and test excavation project took place in Fountain Cavern, Anguilla, from 6–16 January 1986, to assess its prehistoric archaeological resources. The research was undertaken at the request and with the cooperation of the Anguilla Archaeological and Historical Society (AAHS) and Government of Anguilla because Fountain Cavern is being considered for development as an interpretive center. Several surveys evaluating various scientific aspects of Fountain Cavern have been summarized in a recent volume (Gurnee, 1989) produced by the National Speleological Foundation.

Reports to AAHS and Government (Watters, 1986, 1987, 1989*a*) included recommendations for integrating archaeological resources in Fountain Cavern with aspects of local natural history in an above-ground visitors center designed to serve as an educational facility for Anguillians and tourists alike.

Physical Setting

Anguilla lies on the Anguilla Bank in the eastern sector of the Caribbean Sea and is one of the northernmost islands in the Lesser Antilles, which stretch from Grenada in the south (lat. 12°N) to Sombrero in the north (lat. 18.5°N). Anguilla lies only 125 km east of the Virgin Islands, the easternmost islands in the Greater Antilles in the northern Caribbean (Fig. 1).

The Anguilla Bank is the largest bank in the Lesser Antilles, with an area of about 4660 km^2 within the 200 m isobath. The islands of Anguilla, St. Bartholomew, and St. Martin are the main emergent features on the bank. St. Martin is situated about 10 km south of Anguilla. Most of the bank is submerged at depths

Submitted 20 August 1990.

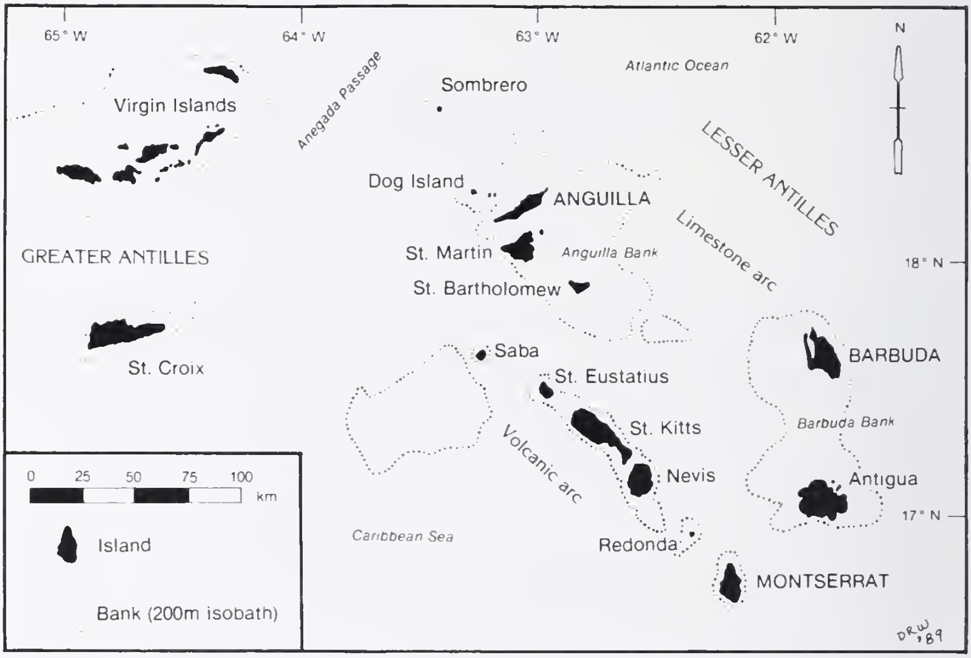


Fig. 1.—Islands and banks of the northeastern Caribbean Sea (eastern Greater Antilles and northern Lesser Antilles).

of 40 m or less (Martin-Kaye, 1969:185). Vaughan (1916:58, fig. 2–4; 1919:303, fig. 11, 19) regarded Anguilla as an example of a "third type" submarine profile, characterized by rocks dipping under the sea at gentle angles and by shores off which are shallow flats. However, deep-water passages isolate the Anguilla Bank from other banks in the region, including the nearby Barbuda Bank (passage depth >200 m) and Saba and St. Eustatius banks (>500 m), while the even deeper Anegada Passage (>2000 m) divides it from the Virgin Islands (excepting St. Croix) of the Greater Antilles (American Geographical Society, 1960).

Anguilla (including nearby Scrub Island) is approximately 30 km (18.6 mi) long. Its maximum width (due E–W) is about 9.3 km (5.8 mi) between Flat Cap Point and Mimi Bay; the maximum width (due N–S) is 6.1 km (3.8 mi) from near Shoal Bay to Forest Point; and the maximum width measured NW–SE, at a right angle to the northeast trending axis of the island, is 5.9 km (3.7 mi) from midway between Blackgarden Bay and Shoal Bay on the north coast to High Cliff on the south coast (Fig. 2). Anguilla has a land area of about 91 km² (35 mi²) and is located between lat. 18°10′ to 18°18′N and long. 62°56′ to 63°10′W (Directorate of Overseas Surveys, 1972, 1973). Being a dry and relatively flat carbonate island, Anguilla exemplifies the low islands in the "Limestone Caribbees" forming the outer arc of the northern Lesser Antilles. The limestone islands differ physiographically from the volcanic islands of the inner arc (Fig. 1), and aspects of the prehistory of these two island arcs also differ (Watters, 1980:334–341).

Anguilla's surficial geology consists almost exclusively of limestone, in what has been termed a "complete carbonate cap" (Adey and Burke, 1977: fig. 2). The term "Anguilla Formation," denoting the island's limestone and marl deposits, was formally proposed by Vaughan (1918:271, 1926:351) based primarily on his study of its fossil corals, although he acknowledged the work of earlier geologists (e.g., Cleve, 1871; Spencer, 1901). The limestone, Lower Miocene in age, is about 75 m (250 ft) thick and lies unconformably over volcanic rocks now regarded as Eocene or Oligocene in age (Christman, 1953:89, 92) and equivalent to St. Martin's Pointe Blanche Formation (cf. Martin-Kaye, 1959:43, 1969:185–186).

Restricted volcanic exposures (Fig. 3) occur on Anguilla, Dog Island some 15 km distant, and its tiny outlier Middle Cay. Initial identifications of igneous rocks on Anguilla at Crocus Bay and Road Bay, respectively as "altered andesitic tuff" (specimen L.I. 99) and "altered basalt" (L.I. 102) (Vaughan, 1926), were verified by Christman (1953:92). Limited information on the igneous rocks of Dog Island and Middle Cay is found in Martin-Kaye (1959:44, 1969:188).

A discontinuous ridge trending northeast parallels the north coast of Anguilla. Goodell (1989:17) indicated the north coast consists of a series of differentially uplifted fault blocks. The island's highest elevation, approximately 200 ft (61 m), is attained on this ridge, midway along the north coast and slightly inland from Crocus Bay. Vertical escarpments some 100 ft (30 m) high mark the north face of the ridge at several places along the coast (Fig. 4A). Sea caves penetrate the base of these escarpments.

The highland or upland topographic area around the ridge contrasts markedly with the central and southern parts of Anguilla. The central part consists of slightly depressed basins, especially near The Valley and Cauls Pond, which in turn are bordered by a low ridge gently descending to sea level along most of the south coast. In the western part of the island where there is no basin, the north coast ridge slopes gradually downward to the south shore. Almost all of the south coast is less than 8 m (<25 ft) above sea level. White-sand pocket beaches (Fig. 4A) are found in most embayments around the island. In western Anguilla, extensive beaches are found along the north and south coasts (Fig. 4B), while smaller beaches occur elsewhere on the north coast at Road Bay, Crocus Bay, and Shoal Bay.

The north, cliffed face of the northeast trending ridge has exposures of highly fossiliferous limestones and marls. Vaughan (1926:351–355) described several geological sections along that coast with a thick argillaceous limestone deposit containing many fossils, mostly of reefal corals and echinoids, underlying a hard cavernous limestone with few or no fossils. Fossiliferous limestone is rare elsewhere in Anguilla. Christman (1953:92) indicated the hard, cavernous limestone is the most widespread; it weathers to a very rough, karst-like surface (Fig. 5). Harris (1965:23) stated that karstic erosion on Anguilla is advanced.

Anguilla's soils have not been studied in detail. Harris (1965:23–24), as part of a broader ecological study of the island, identified two soils, a reddish-brown stony clay *terra rossa* in the uplands and a gray to black, ill-drained rendzina in lower areas. Goodell (1989:18) described the soils as generally thin and lateritic. Soil accumulation is greatest in the basins and solution depressions but it is limited all across the island. Bare limestone pavement protrudes throughout Anguilla and is especially prominent on the east and west headlands.

Rainfall is limited and seasonal. Annual rainfall varies but averages about 1040 mm (Martin-Kaye, 1959:43; Harris, 1965:9; Howard and Kellogg, 1987:106) and is greatest in The Valley in the island's center (Eastern Caribbean Natural Area Management Program, 1980: map 2). May and August through November are

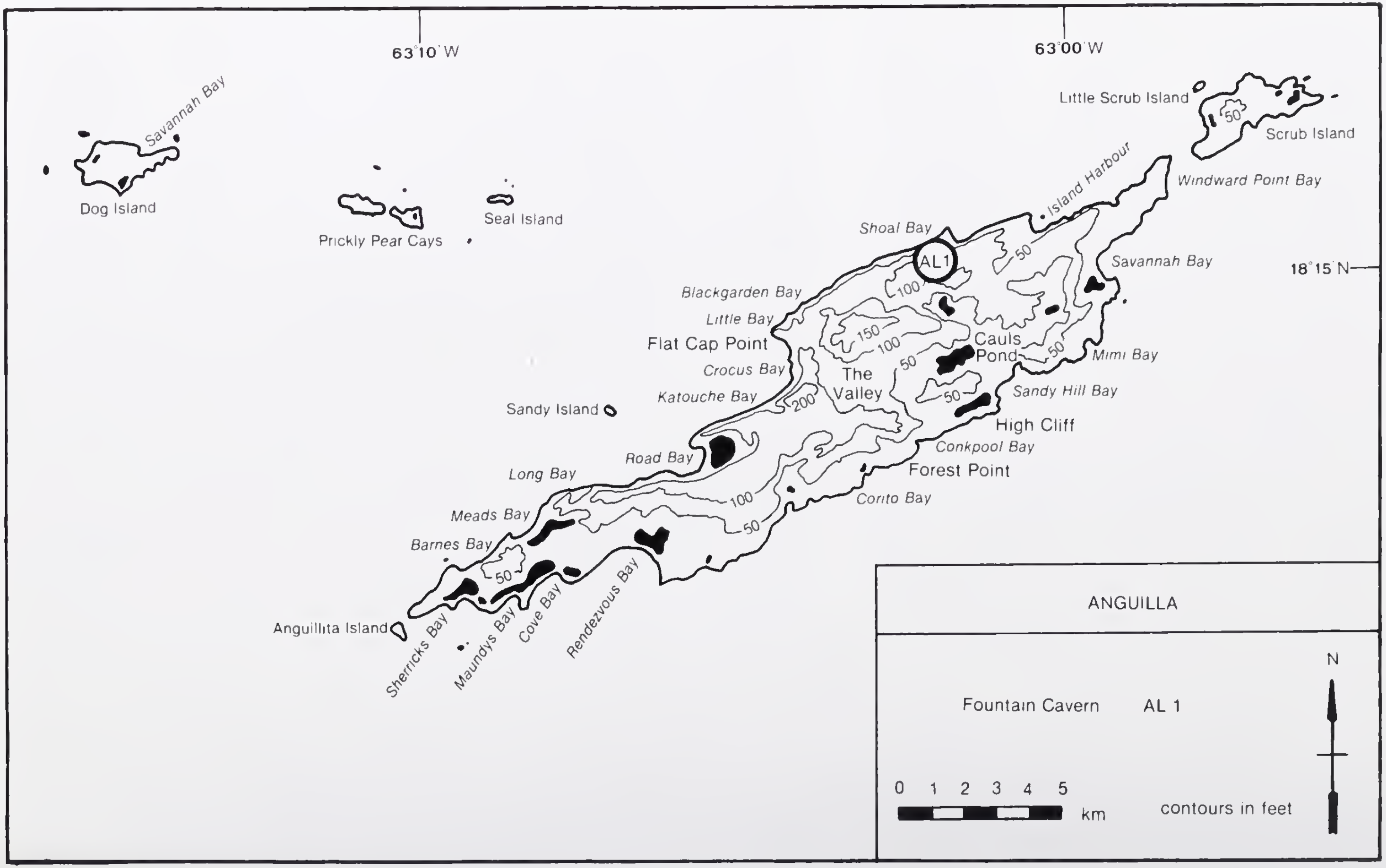


Fig. 2.—Topography of Anguilla and location of Fountain Cavern (AL1) prehistoric site.

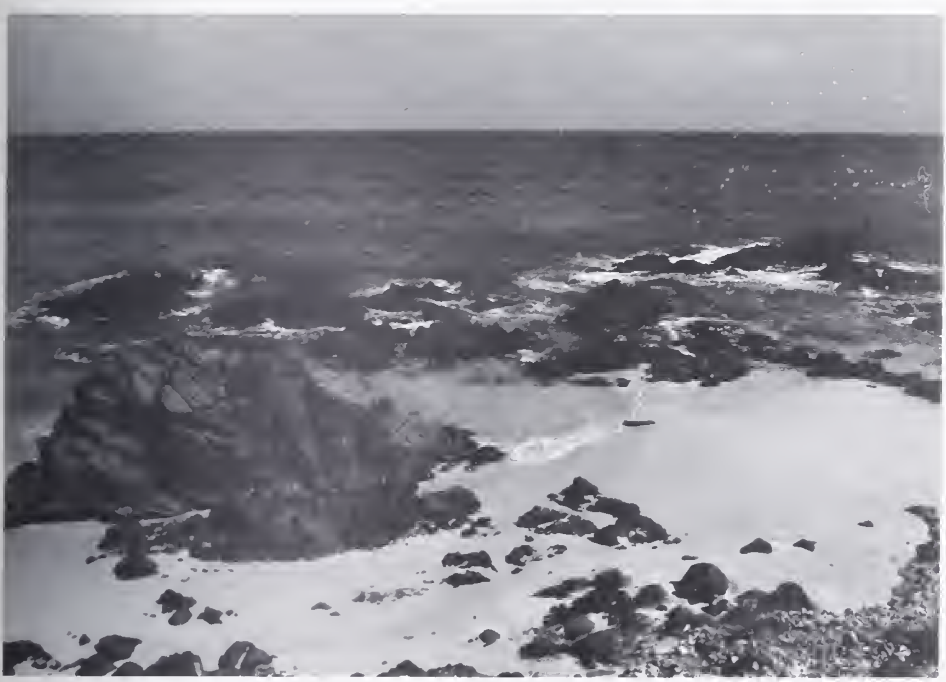


Fig. 3.—Outcrops of igneous rock at Savannah Bay beach, Dog Island.

peak precipitation months, a pattern which pertains throughout the northern Lesser Antilles. Rainfall disperses mainly through infiltration into solution fissures and sinkholes. Anguilla has no surface streams.

Anguilla's vegetation recently was studied by Howard and Kellogg (1987). Harris (1965:41–42, 137) classified Anguilla's dominant vegetation as "very degraded evergreen woodland," which he regarded as a subclimax induced by ". . . biotic processes of impoverishment and selection of xerophytic, sclerophyllous species . . ." rather than the island's "natural" vegetation. Beard (1955) concluded that the "evergreen bushland" is the natural vegetation, a point of view also favored by Howard and Kellogg (1987:107, 111). Harris (1965:50–53, fig. 12) also mentioned small areas of grassland, manchineel, and mangrove, as well as strand and rock pavement vegetation.

FOUNTAIN CAVERN

Fountain Cavern (also known as The Fountain) is located in the first national park created by the Government of Anguilla. The park, founded in 1985, is situated at Shoal Bay on Anguilla's north coast (Fig. 2). It encompasses about 1.9 ha (4.75 a) and extends from the shoreline to Fountain Hill. Fountain Cavern lies 250 m inland in the southern part of the park at coordinates (approximate) 906185 on the British West Indies Grid (Directorate of Overseas Surveys, 1972, 1973).

The area around Fountain Hill is credited by Anguillians with more rainfall than many other areas of the island. Various plant communities occur within the national park's boundaries, from the shoreline to the higher elevations inland. G. Douglas (1989) reported 62 plant species within the park's borders.

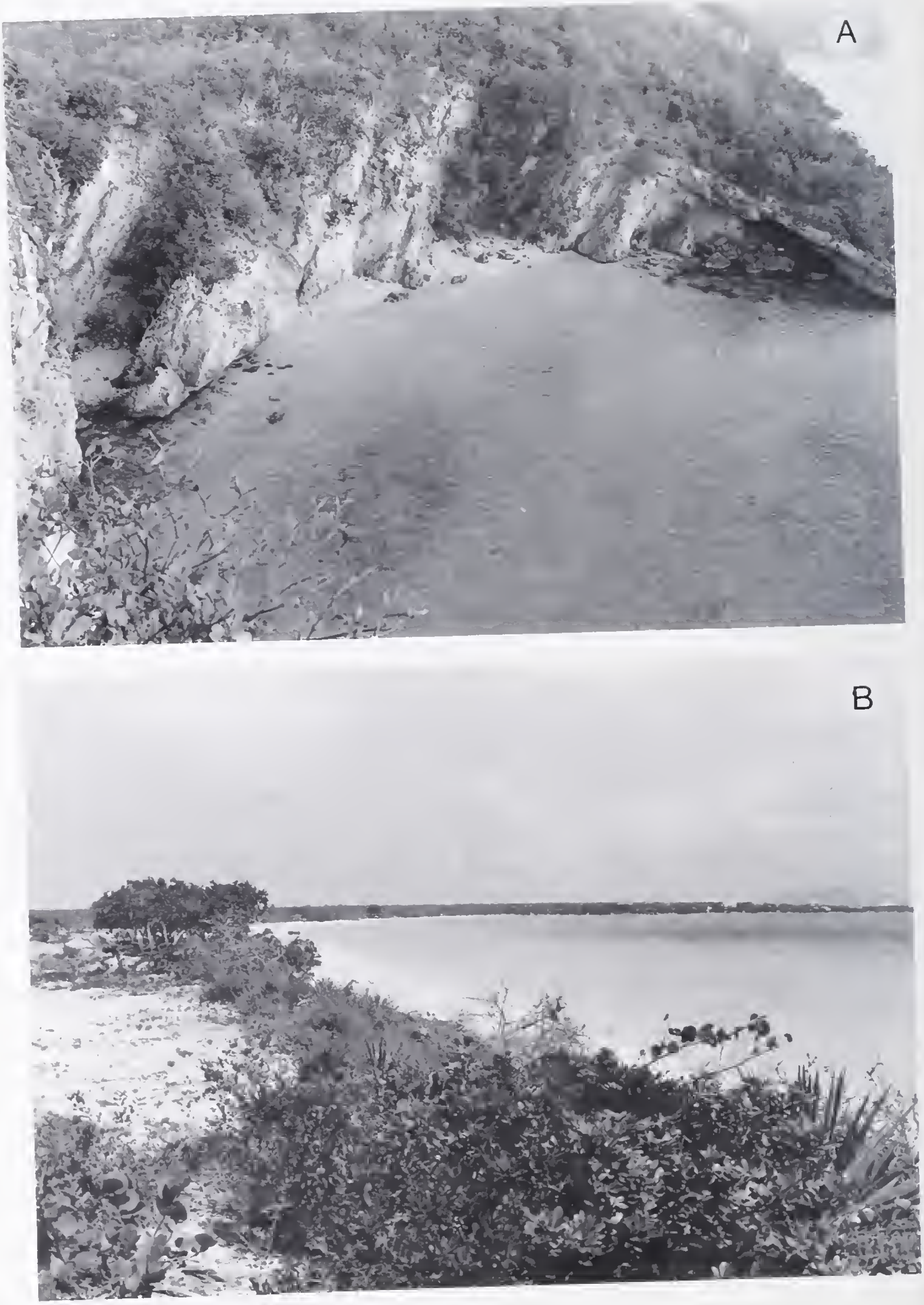


Fig. 4.—A. Cliffs and pocket beach at Little Bay, north coast of Anguilla. B. Rendezvous Bay beach on Anguilla's south coast, with the mountains of St. Martin visible in the background.

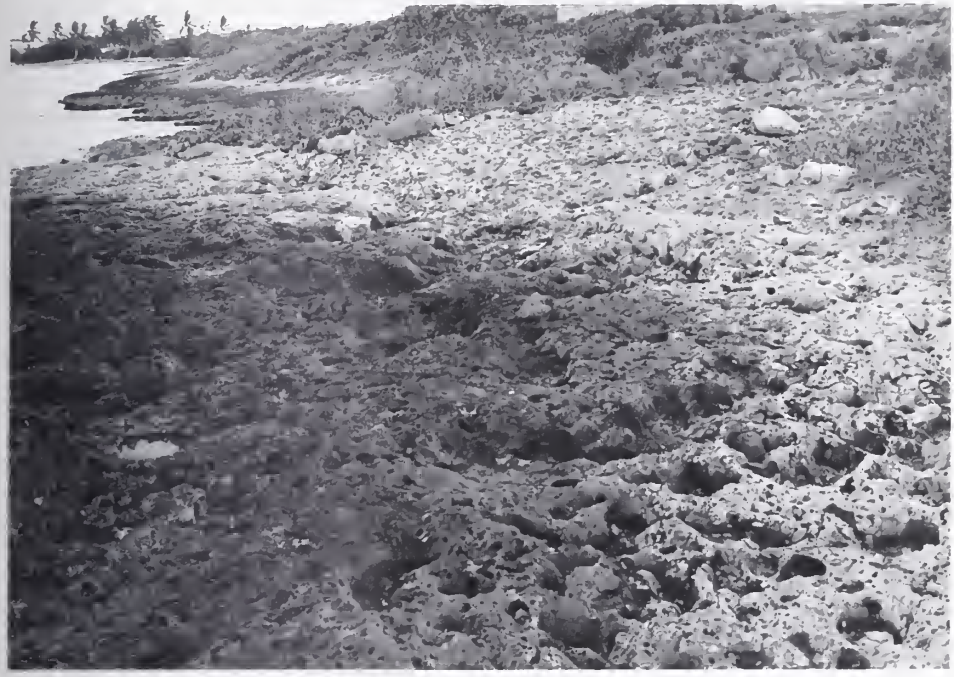


Fig. 5.—Weathered limestone at Island Harbour, northeast coast of Anguilla.

Until 1989, few published reports about Fountain Cavern were available. Wagenaar Hummelinck (1979:165–168) briefly discussed Fountain Cavern and provided two maps (a longitudinal section and ground plan) as well as a photograph of the entrance. Background information on Fountain Cavern and the creation of the national park is found in several articles in the *Anguilla Archaeological and Historical Society Review, 1981–1985* (N. Douglas, 1986*c*). In 1989, summary reports of the archaeology, geology, vegetation, and bats, a proposal for developing the national park, and plan views and profiles of the cavern were published (Gurnee, 1989).

Fountain Cavern occurs in the hard, cavernous limestone on the north slope of the northeast trending ridge at an elevation of about 18 m (60 ft). Goodell (1989:17–18) indicated the cavern is located in a well-indurated Miocene biohermal and biostromal limestone that is cream to buff colored except where weathered to a light gray. It is a vaulted or domed cavern with a maximum length (SW–NE) of about 50 m and width (NW–SE) of approximately 30 m. The cavern entrance is a relatively small hole (ca. 2 × 3 m) in the ceiling, about 10 m above a generally level area. A steel ladder installed in 1953 shares the entrance with long tree roots (*Clusia* sp.) that previously provided the means of access. The cavern is humid and poorly ventilated.

Fountain Cavern is divided into two distinct chambers (Fig. 6). Chamber 1 includes the area under the entrance, the domed ceiling in the front of the cavern, and Pool 1; it reaches a maximum height of about 15 m and has a steeply sloping

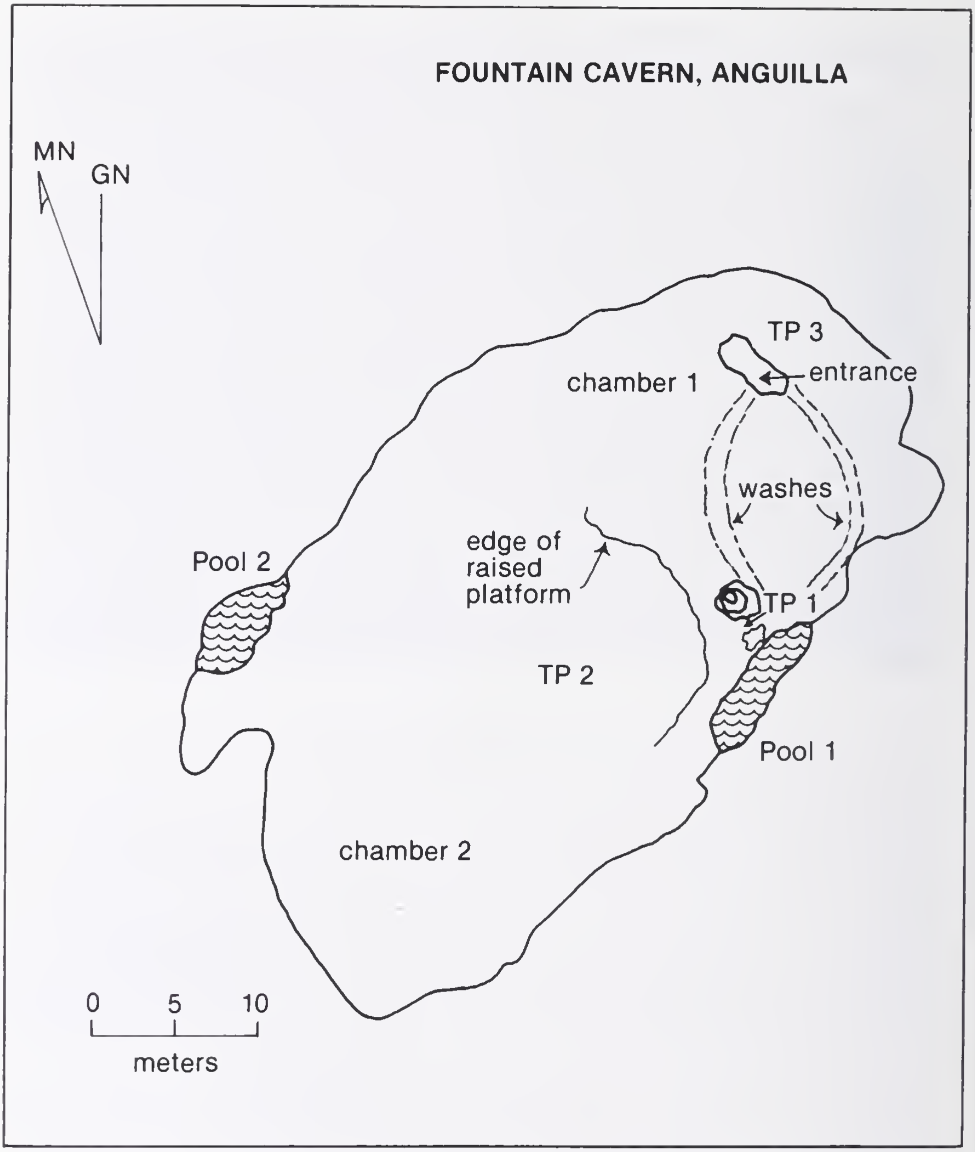


Fig. 6.—Generalized planview of Fountain Cavern showing the positions of chambers and test pits.

floor. Chamber 2 begins at a raised platform in the middle of the cavern and continues westward to its deepest recesses near Pool 2. A low entrance (ca. 4 m high) into Chamber 2 occurs at the edge of the raised platform where the roof dips downward, a constriction resulting from a large limestone roof pendant from which is suspended a large stalactite (Goodell, 1989:18). In Chamber 2, the roof rises only slightly and the floor is fairly flat. Light in Chamber 1, the only part of the cavern where sunlight enters, is subdued. A colony of bats resides in Chamber 2 where almost no light penetrates. One bat species, *Brachyphylla cavernarum* (Antillean cave bat), was captured within Fountain Cavern and another species, *Natalus stramineus* (funnel-eared bat), was taken near the entrance (Genoways, 1989). Very sizeable speleothems (columns and stalagmites) are present on the raised platform, at least three of which remain upright although several others have toppled (Fig. 7A). Water elevation in Pool 1 is 19.4 m, and in Pool 2 is 20.4 m, below the surface benchmark (Goodell, 1989:18). Anguillians have long known of the existence of Fountain Cavern and local legend holds that water always could be obtained from its pools, even during the worst droughts.

Differences other than roof height exist between the two chambers. The floor of Chamber 1 slopes sharply downward to the southeast, south, and southwest from the relatively level area beneath the entrance (Fig. 7B). Goodell (1989:18) described this slope as a debris cone. North of the area beneath the entrance, the floor rises slightly and is covered by large rocks detached from the roof. The floor of Chamber 2 on the raised platform in the middle of the cavern is elevated above most of Chamber 1. The floor remains fairly flat until it reaches the western sector of the cavern where it drops steeply to Pool 2.

Extensive spalling from the roof and walls has occurred in Chamber 1, where many rocks have rolled downslope and come to rest in piles against the south and southeast walls. The piles contain large limestone rocks and chunks of broken speleothems. Goodell (1989:18) indicated the debris accumulated mainly from roof breakdown and ranges from blocks several meters in diameter to much smaller bedding plane slabs and chips to sand and silt. Spall and roof falls in Chamber 2 are scattered across the raised platform rather than being concentrated in piles. The abundance of spall, toppled columns, and broken stalactites indicates that major disturbances, probably earthquakes, have severely wrenched Fountain Cavern in the past. Most stalactites still attached to the ceiling have broken tips.

Sediment depths differ between Chambers 1 and 2. In Chamber 1, major deposits occur beneath the entrance, on the slope, and against the south and southeast walls. Beneath the entrance and on the upper slope the deposits are mainly fine-grained sediment, but at the bottom of the slope and against the walls the deposits are chiefly fragmented rocks. Sediment that accumulated under the entrance has been transported downward along two "washes" bordering the slope (Fig. 6). Gradual downward movement, water runoff from rain falling through the entrance, and treading by people using the washes as trails have contributed to downslope transport of sediment. Sediment deposition in Chamber 2 is negligible and consists mainly of decomposing limestone bedrock covered by bat guano.

Prehistoric archaeological components of Fountain Cavern were known prior to the 1986 research. Petroglyphs were first noted in 1967 by June Flowers from St. Thomas, U.S. Virgin Islands (Dick et al., 1980:35; Douglas, 1986*b*:27). In 1979, a team from the Island Resources Foundation verified the presence of artifacts and petroglyphs in Fountain Cavern (Island Resources Foundation, 1980; Dick et al., 1980). During the 1980s the Anguilla Archaeological and Historical Society collected surface artifacts and recorded 12 petroglyphs at the site (Douglas, 1985, 1986*a*, 1989). AL1 is the site designation for the Fountain Cavern prehistoric site.

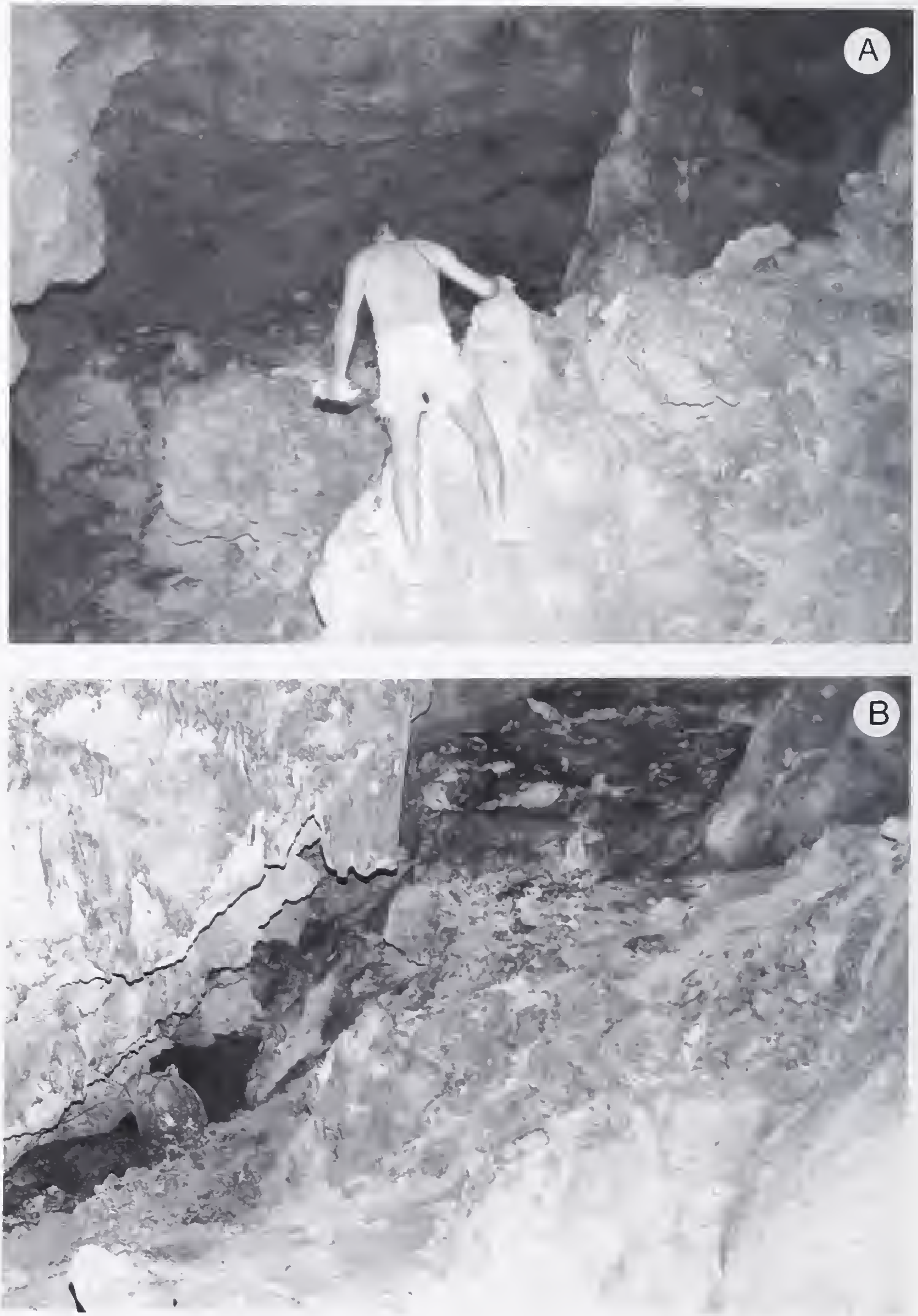


Fig. 7.—A. View (looking WSW) of the raised platform and columns in Chamber 2, Fountain Cavern. In the foreground, the large stalagmite with Petroglyph 12 is being measured. B. The sloping floor of Chamber 1 leading to the large stalagmite (with Petroglyph 12) and truncated column (Petroglyph 11) with Pool 1 behind.

METHODOLOGY

The archaeological research in Fountain Cavern involved: a general reconnaissance of the cavern; a survey of the locations of surface artifacts; an examination of petroglyphs; excavation of three test pits; and analysis of recovered artifacts and faunal remains. The research was intended to provide an overview of horizontal distribution of artifacts in the cavern and information about depths of cultural deposits in selected areas, and to determine the temporal and cultural affiliations of artifacts. Spatial data were recorded initially on sketch maps and then transferred to surveyed plans once they became available. The majority of the fieldwork was devoted to test excavations.

Analysis of the artifacts and faunal remains, radiometric dating of shell and carbon samples, preparation of interim reports, and cataloging and photographic documentation of the Fountain Cavern collection have taken place in the United States since 1986. Fountain Cavern's Amerindian ceramics are the focus of a separate report (Petersen and Watters, 1991).

ARCHAEOLOGICAL SURVEY

Archaeological materials on the floor of Fountain Cavern were confined largely to Chamber 1. Surface artifacts were observed in the level area beneath the entrance, in the washes on the slope, along the south wall, and in the vicinity of Pool 1 (Fig. 6).

Chamber 2 produced very few surface artifacts. Given the very shallow depth of sediments on most of the floor in Chamber 2, it is unlikely that any substantial cultural deposits are present; however it is possible that some fissures in Chamber 2 may contain artifacts.

Abundant surface artifacts were observed in two areas of Chamber 1. The first, a relatively flat area termed "Surface Area A," was located at the base of a large stalagmite, atop which is an impressive carving recorded by the AAHS as petroglyph #12 (Douglas, 1985:10, 1986*a*:3, 1989:13). Surface Area A extends from between the stalagmite and a nearby truncated column with petroglyph #11 (immediately adjacent to Pool 1) eastward about 6 m to the western wash on the slope. In this area the AAHS had removed artifacts from piles of loose rocks at the base of the stalagmite and thereafter replaced the rocks to mask the obvious concentration of artifacts in that location (Fig. 8A).

The second area, "Surface Area B," was located along the south wall of the cavern. The eastern wash curves toward the southwest by the south wall and most of Surface Area B was located between the wash and the wall, just east of Pool 1. Artifacts were intermingled with sediment and spall deposits piled against the wall. Artifacts also were recovered in a partially water-filled cavity at the east edge of Pool 1.

Based on the results of the archaeological survey and the previous work undertaken by the AAHS, it was decided to focus initial testing in Chamber 1, to be followed by a check of the shallow sediments in Chamber 2. Actual placement of test pits was determined by the: (1) density of surface artifacts collected by the AAHS; (2) observation of surface artifacts by Watters; (3) depth of the sediments; (4) proximity to washes with evidence of downslope transport; and (5) spatial relationship to petroglyphs.

TEST EXCAVATIONS

Three test pits were excavated in Fountain Cavern, two in Chamber 1 and one on the raised platform in Chamber 2 (Fig. 6). All test pits were 1 × 1 m and

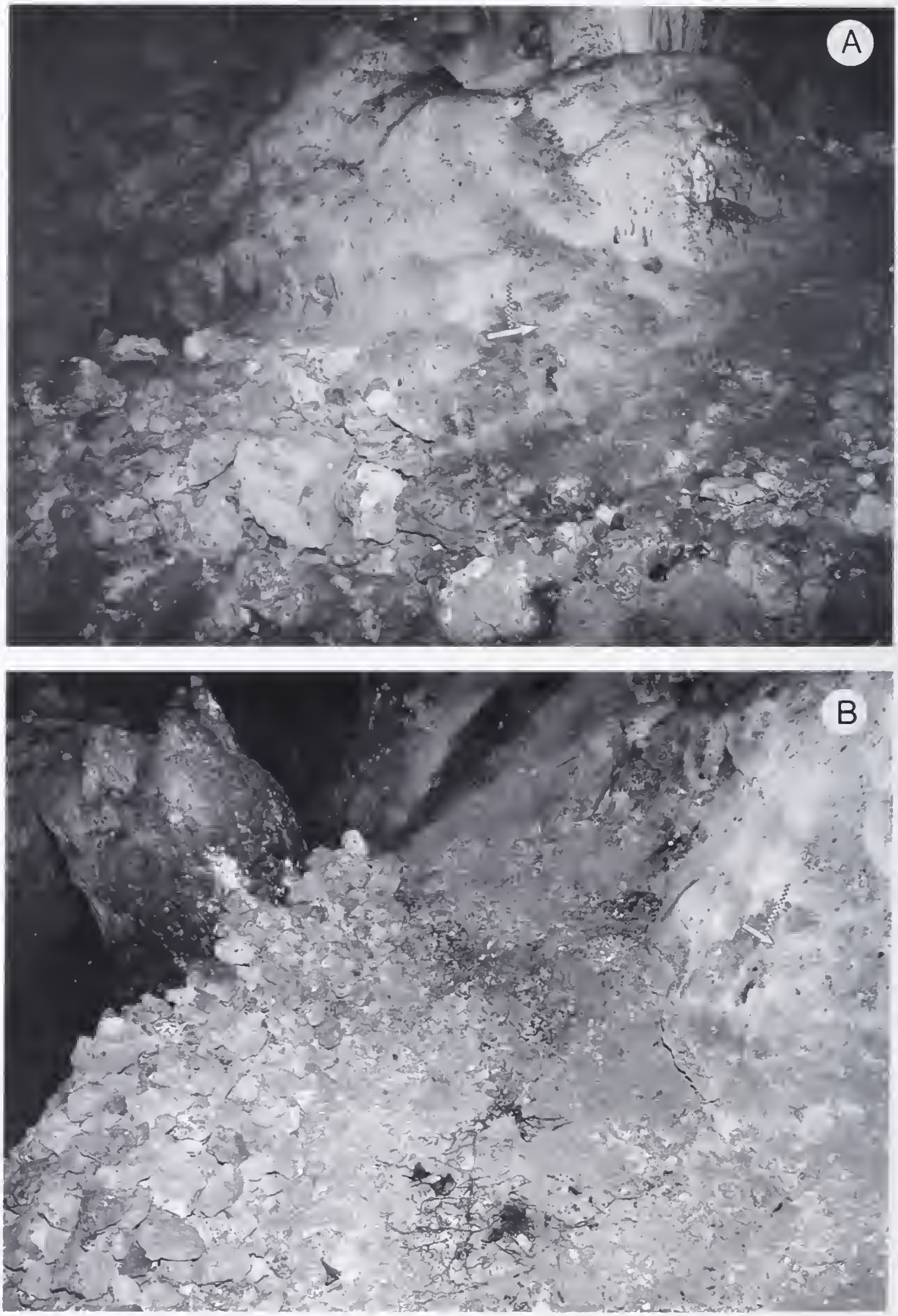


Fig. 8.—A. Loose rocks piled by the AAHS at the base of the large stalagmite to mask the surface artifact concentration (in Surface Area A). B. Test pit 1 was dug between the stalagmite (right) and truncated column (left) behind the loose rocks piled into a retaining wall.

aligned to fit between nearby obstacles. They were dug to bedrock and all natural and cultural materials were removed. Deposits were screened through ⅛-inch mesh; recovered materials were segregated by unit.

Test Pit 1

Test pit 1, in the southwest section of Chamber 1, was positioned at the base of the south side of the large stalagmite with petroglyph #12 carved at the top and on the north side of a nearby truncated stalagmite (with petroglyph #11) adjacent to Pool 1. The 60-cm-high pile of rocks, placed there previously by the AAHS, was removed and the rocks were used to form a retaining wall to stop debris from sliding into Pool 1 (Fig. 8B). Artifacts found among these rocks and on the surface near the stalagmites were assigned to "Surface Area A." The four corners of test pit 1 were laid out on cardinal directions using magnetic north, and the walls were offset (at 045°) to position the test pit between the stalagmites. Walls were designated as northeast, southeast, southwest, and northwest.

When the surface of test pit 1 was exposed after removal of the rocks, a shallow (ca. 5 cm) layer of light yellowish brown (Munsell notation 10 YR 6/4 dry) sediment (Stratum 1) was observed across the test pit (Fig. 9). However, Stratum 1 had a definite reddish cast in the west corner of the test pit, and in the north corner was a slight depression, the remnant of a shallow hole dug into the surface in the past, that extended eastward beyond the confines of the test pit. Test pit 1 initially was horizontally segregated into three sectors: (1) Sector A in the west corner by the reddish sediment; (2) Sector C, the depression, in the north corner; and (3) Sector B, the remainder of the pit (essentially the southeast half). In the upper portion of the test pit each sector was excavated individually, but at a depth of about 50 cm the sector distinction was abandoned because variations in sediment color and texture were no longer discernible.

Stratum 2, in Sector A, was reddish brown (5 YR 4/4), extended horizontally about 50 cm into the test pit, was visible in the southwest and northwest profiles (Fig. 9), and reached a maximum depth below surface of 30 cm. It was immediately adjacent to a reddish flowstone deposit in the southwest wall. Stratum 3, the most limited of the strata, occurred in the southwest wall but only in the southern half of the pit, in Sector C. It reached a maximum depth of about 10 cm adjacent to Stratum 2 but feathered out before reaching the south corner of test pit 1 (Fig. 9). Stratum 3 was patchily distributed rather than being a uniform layer. Its color was yellowish red (5 YR 5/6).

Stratum 4 (brown, 7.5 YR 5/4) directly underlaid Stratum 1 in Sectors B and C, was the principal deposit in test pit 1 (to a depth of about 155 cm), and consisted mostly of spall, primarily fragmented rocks and broken speleothems (Fig. 9). Interspersed in cavities among the rocks were patchy accumulations of finer sediments. The excavation technique involved removing the rocks by hand and then gathering together the limited amounts of fine sediment for screening. Four large rocks occurred in test pit 1 (Fig. 10). Rocks 2 and 3 each protruded into one of the walls and, when removed, caused the walls to slump. Rock 4, wedged across the bottom of test pit 1, had to be left in place because removing it would have collapsed the walls.

Excavation was complicated by intrusion of the stalagmite (with petroglyph #12) into the pit (Fig. 9). As test pit 1 was dug deeper, the stalagmite encroached or protruded farther into the test pit from the northwest profile. By the time test pit 1 "bottomed out," the stalagmite occupied almost 50% of the area, and most

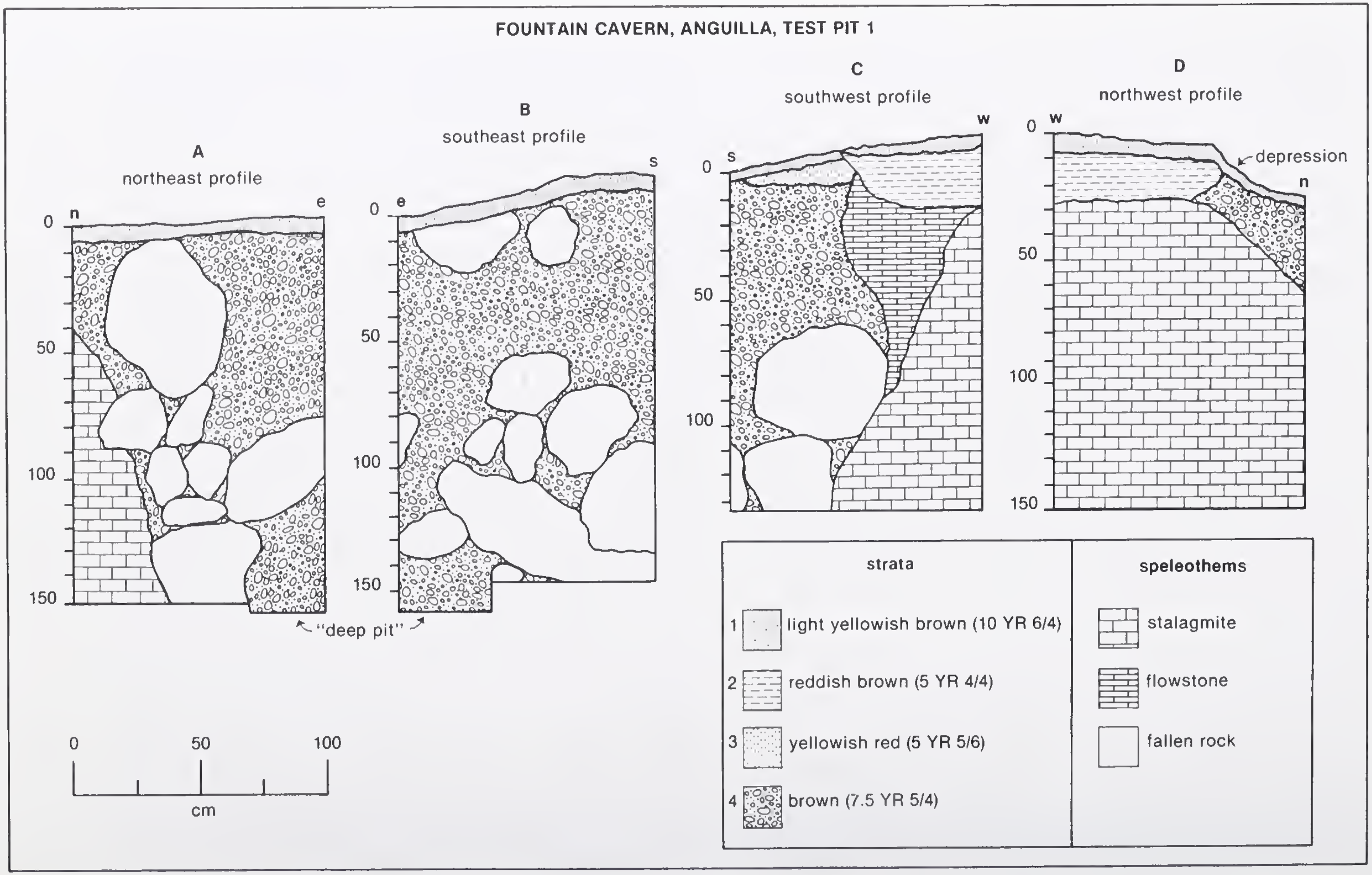


Fig. 9.—Four profiles of test pit 1, Fountain Cavern.

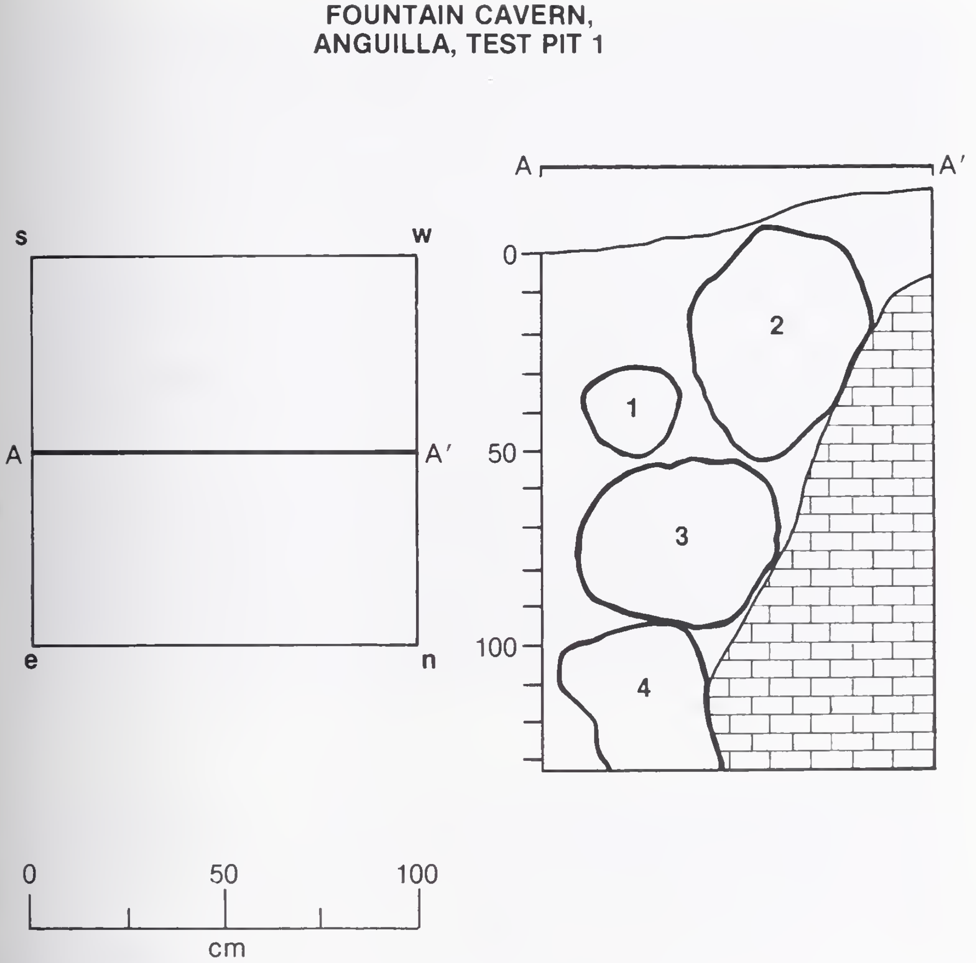


Fig. 10.—Large rocks under line A-A′ bisecting test pit 1. Rock 1 was within the test pit's borders, Rock 2 penetrated the northeast wall, Rock 3 the southwest wall, and Rock 4 (wedged and immovable) both walls.

of the rest of the base was taken up by Rock 4, wedged in the bottom. Only a 20 × 30 cm area (the "deep pit") in the east corner remained accessible for excavation (Fig. 11). When bedrock was reached at about 155 cm (Fig. 12), water seeped into the deep pit from nearby Pool 1.

The intrusion of the stalagmite, the presence of large rocks, and the increasingly narrow and restricted space for digging meant that tight vertical control could not be maintained throughout test pit 1. As a result, the uniform 10-cm excavation units dug in Sector A of the test pit were impossible to maintain when the mass of large rocks was encountered. Between the base of Rock 2 and around most of Rock 3, from about 50 to 90 cm (Fig. 10), vertical control was minimal because as each rock was removed from the test pit, part of the wall in which it was embedded slumped, causing materials from the walls to slide into the test pit. Plastic sheets were placed under the rocks to catch these wall falls, thereby allowing

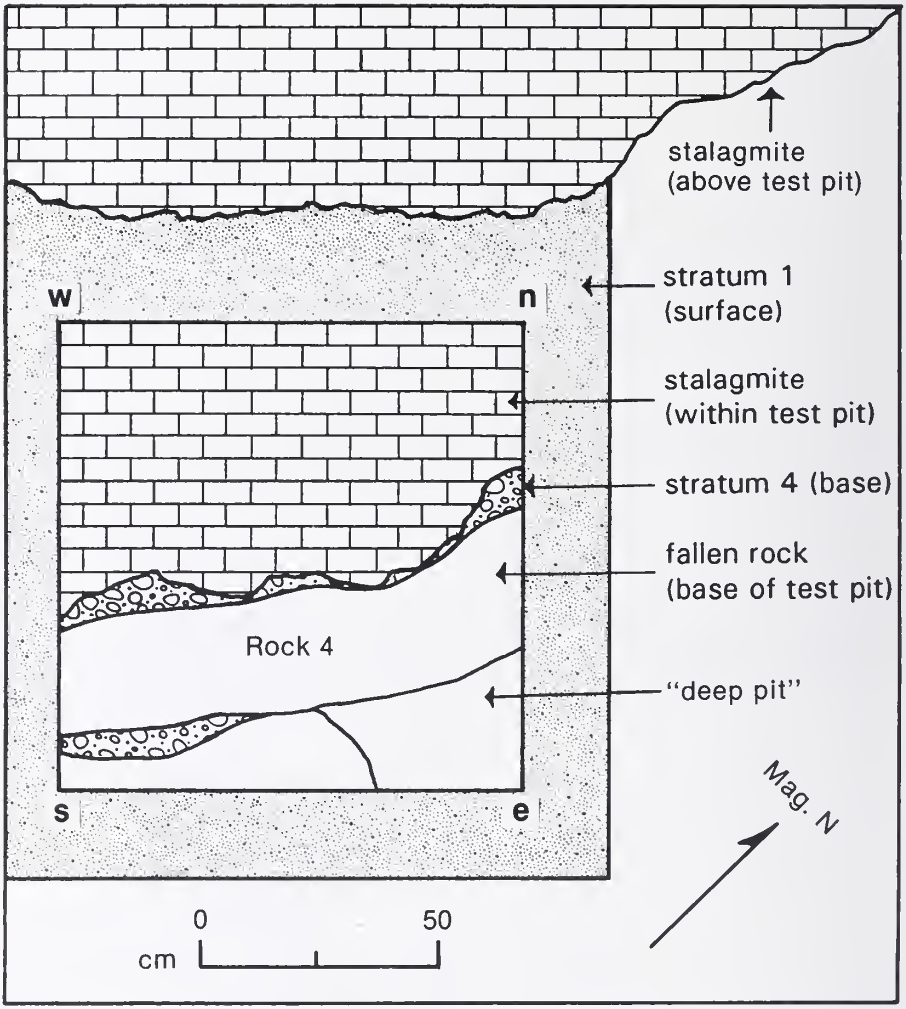


Fig. 11.—Planview of the area around test pit 1 showing the intrusion of the stalagmite from the northwest wall (see also Fig. 9 and 10). The "deep pit" was the bottom of test pit 1.

them to be removed and segregated as "wall debris." Table 1 shows the provenience of excavated units and code numbers applied to each.

Cultural materials were found throughout test pit 1. Yet, artifacts from radically different time periods were intermingled at various depths. Modern artifacts, transported downward through the crevices and holes among rocks in Stratum 4, were juxtaposed with older, prehistoric materials. In one case, in a cavity exposed beneath a rock that was removed at about 50 cm, a prehistoric sherd and a piece of plastic were observed beside one another, along with the still visible striations in the sediment showing where the plastic piece slid into the hole. Trampling and shifting of rocks by people going to Pool 1 most likely caused the downward movement of artifacts; this taphonomic process has probably accelerated in modern times. The mixing of artifacts from different time periods did not result from

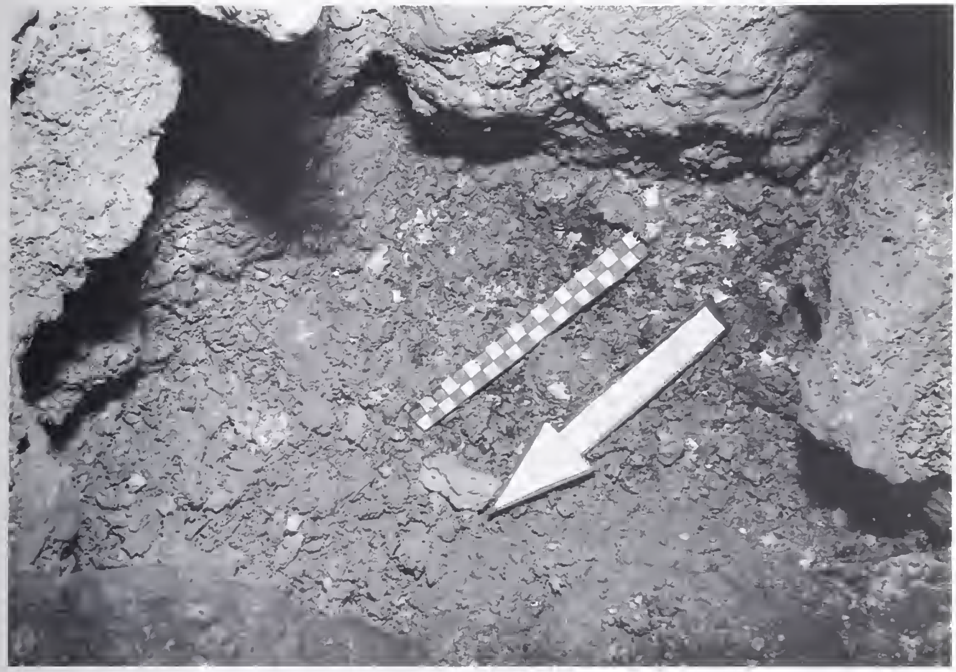


Fig. 12.—When the deep pit (ca. 20 × 30 cm) reached bedrock at a depth of 155 cm, it was moistened by water from nearby Pool 1.

humans having actively dug up or turned over the deposits in the past. Instead, the taphonomic process seems to be an agglomerative one, whereby younger materials have been transported downward and essentially "added" to older artifacts already "in place" in the crevices of the lower deposits. The extent of downward movement of artifacts is documented by modern objects, such as glass fragments and coins having quite recent dates, that were recovered deep in test pit 1.

Test Pit 2

The second test pit was excavated in Chamber 2 on the raised platform in the middle of the cavern (Fig. 6). Test pit 2 was excavated to verify the apparently shallow depth of the sediment and to confirm the paucity of subsurface artifacts. The corners of test pit 2 were laid out on cardinal directions using magnetic north, but again the walls were offset (030°) to fit the surroundings. Profiles were labeled as the northeast, southeast, southwest, and northwest.

Sediment in Stratum 1, the only stratum, was light brownish gray (10 YR 6/2) in color and composed of bat guano and decomposed limestone. Across most of the test pit, sediment depth above bedrock did not exceed 5 cm (Fig. 13), although it was slightly deeper (ca. 8 cm) in a small natural depression in the center (Fig. 14A). Stratum 1 was removed as a single excavation unit. Two partially buried prehistoric pottery sherds were found near the northwest wall. One tiny lizard bone (fresh in appearance) was recovered on the surface.

Table 1.—*Unit codes and original provenience.*

Code number	Provenience
D1-1	Surface Area A
D1-2	Surface Area B
D1-3	Test pit 1, Sector A, 0–10 cm
D1-4	Test pit 1, Sector A, 10–20 cm
D1-5	Test pit 1, Sector A, 20–30 cm
D1-6	Test pit 1, Sector A, 30–70 cm
D1-7	Test pit 1, Sector B, 0–5 cm
D1-8	Test pit 1, Sector B, 5–35 cm
D1-9	Test pit 1, Sector B, 35–50 cm (Rock 1)
D1-10	Test pit 1, Sector C, 0–5 cm
D1-11	Test pit 1, Sector C, 5–50 cm (Rocks 2 and 3)
D1-12	Test pit 1, 90–100 cm ("Good Level")
D1-13	Test pit 1, 100–110 cm ("Good Level + 1")
D1-14	Test pit 1, 110–120 cm ("Deep pit #1") (Rock 4)
D1-15	Test pit 1, 120–130 cm ("Deep pit #2") (Rock 4)
D1-16	Test pit 1, 130–140 cm ("Deep pit #3") (Rock 4)
D1-17	Test pit 1, 140–155 cm ("Deep pit #4") (Rock 4)
D1-18	Test pit 1, all debris from slumping walls
D1-19	Test pit 2, 0–8 cm (entire depth)
D1-20	Test pit 3, Surface (roots)
D1-21	Test pit 3, 0–10 cm
D1-22	Test pit 3, 10–20 cm
D1-23	Test pit 3, 20–30 cm
D1-24	Test pit 3, 30–75 cm (bedrock fissures)
D1-25	Pool 1 by Surface Area B (encrusted sherd)
D1-26	Petroglyph rock (chip)

Test Pit 3

Test pit 3 was dug on the east side of the relatively level area beneath the entrance to Fountain Cavern (Fig. 6). It was not directly below the entrance; instead it was situated under an overhang against the east wall of the cavern. The location (Fig. 14B) was chosen because it was near the entrance to the cavern and a panel of petroglyphs.

The walls of test pit 3 were positioned on the cardinal directions (magnetic north) and labeled as north, east, south, and west profiles. Corners of the test pit were designated northeast, southeast, southwest, and northwest. The ground surface sloped slightly, making the north wall of the test pit about 15 cm higher than the south side.

Matted roots and loose rock covered about 5 cm at the top of test pit 3. Immediately below was Stratum 1, a brown (10 YR 5/3) sediment generally uniform in color (Fig. 15) except immediately above bedrock, where it was a slightly darker brown (10 YR 4/3). Stratum 1 contained roots, leaves, and other organic matter. Several larger rocks were embedded in the walls of test pit 3; a thin layer of smaller rocks occurred above the decomposing bedrock. There were, however, many fewer rocks in test pit 3 than in test pit 1. Although Stratum 1 reached bedrock at 25–30 cm below ground level in some parts of the test pit, further excavation revealed that bedrock occurred at different depths elsewhere in test pit 3, with Stratum 1 extending to 40–45 cm in certain areas (Fig. 16). Stratum 1 was removed in 10-cm layers. Below Stratum 1, fissures penetrated deep into bedrock including an especially deep fissure which reached a depth of

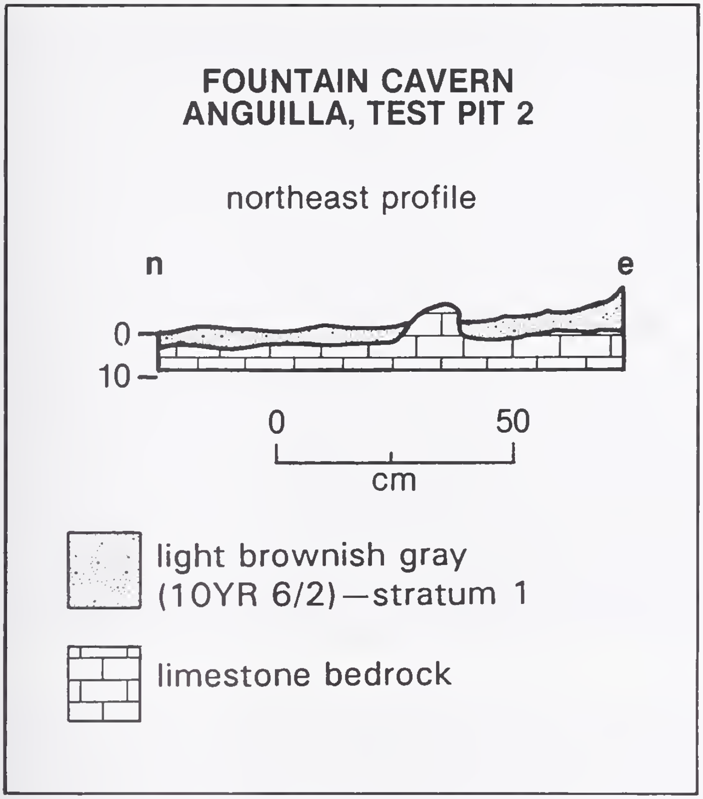


Fig. 13.—Profile of shallow test pit 2, Fountain Cavern.

about 75 cm near the northwest corner (Fig. 16). Stratum 2, consisting of a very fine-grained and very pale brown sediment (ranging from 10 YR 7/3 to 10 YR 8/3), filled these fissures, crevices, and holes.

Artifacts were recovered only from Stratum 1. Prehistoric and historic artifacts were mingled to a depth of about 30 cm; modern objects occurred to 20 cm; these artifacts cannot be regarded as being in primary context. Artifacts and sediments in test pit 3 were mixed during installation of a steel ladder in 1953, when they were dug up, intermingled, and redeposited.

RADIOMETRIC DATING

Radiocarbon dating was done by Beta Analytic, Inc., on two shell samples and one charcoal sample removed from test pit 1 on 11 January 1986. Shells selected for analysis were *Cittarium pica,* a species of marine gastropod widely distributed in the Caribbean. Sherds and other artifacts were found near the shell and charcoal samples.

The first shell (sample AL1-RC1) was recovered at a depth of 50 to 55 cm below ground surface, between the stalagmite and base of Rock 2 (Fig. 10) about 22 cm from the north stake and 10 cm in from the northwest profile. Five shells were clustered at this location. It yielded a radiocarbon age of 1220 ± 70 years: A.D. 730 (Beta-15485). (All dates are uncorrected.)

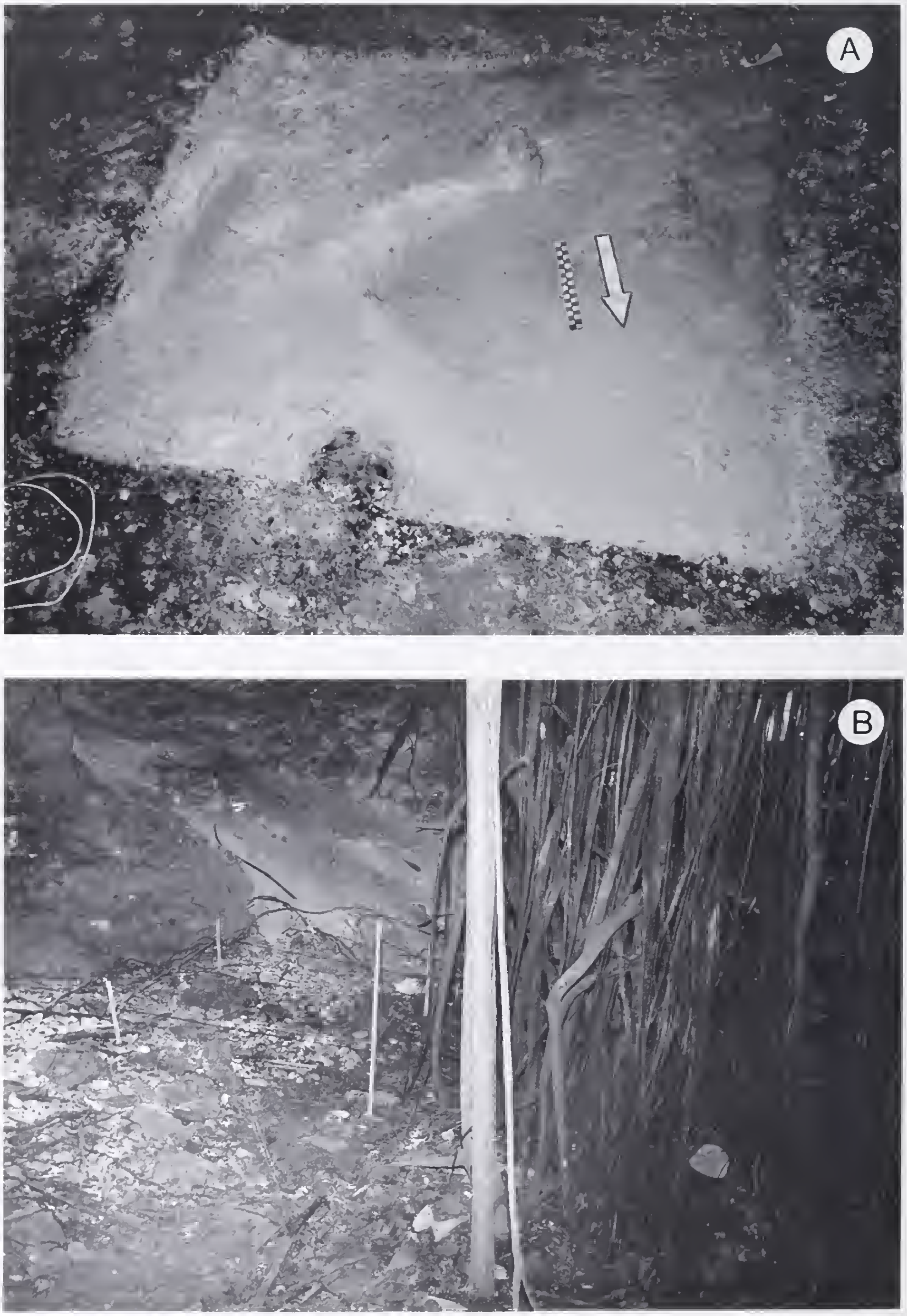


Fig. 14.—A. Completed excavation of test pit 2 showing a small natural depression in the center. B. Location of test pit 3 near the tree roots and ladder beneath the entrance.

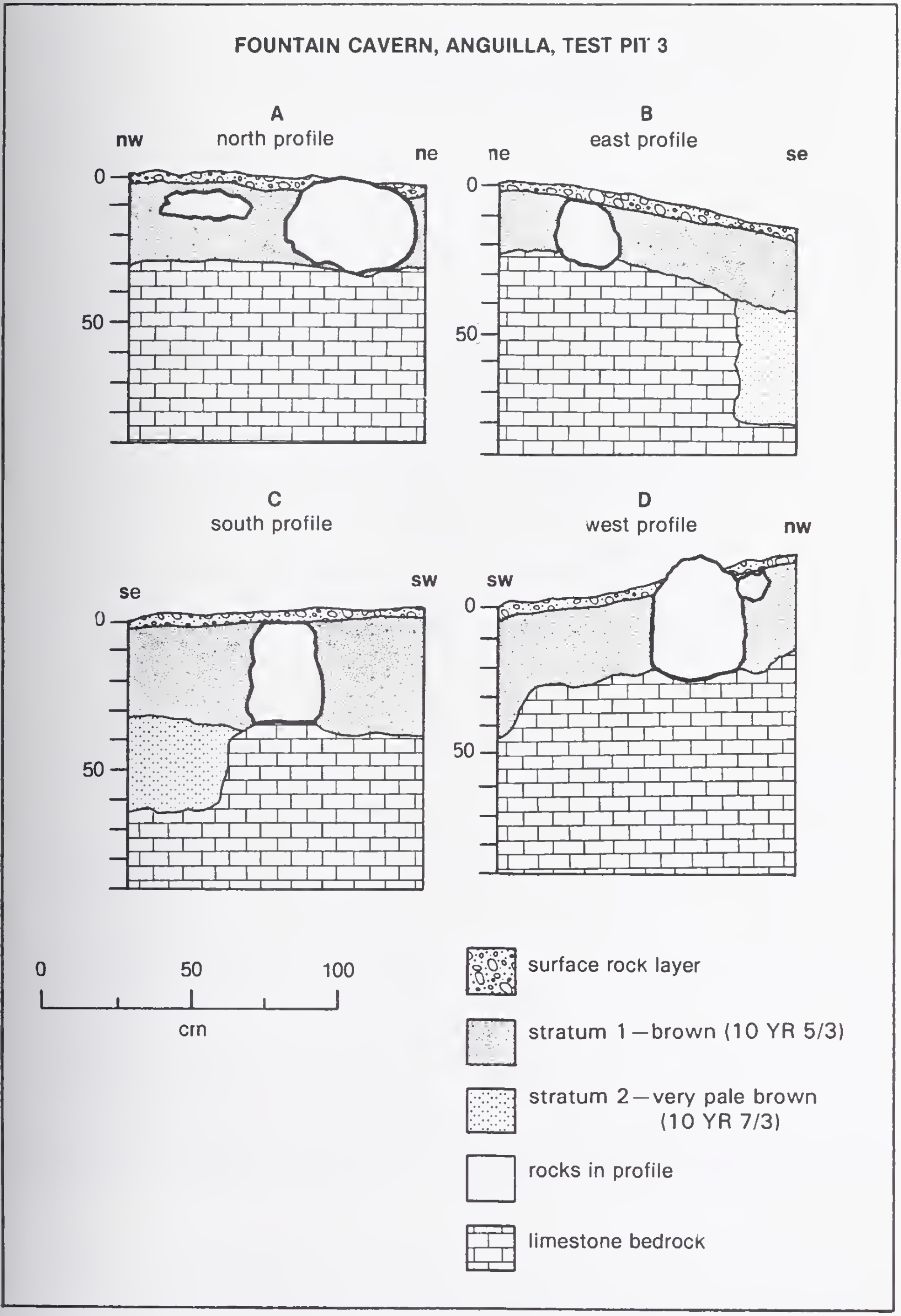


Fig. 15.—Four profiles of test pit 3, Fountain Cavern.

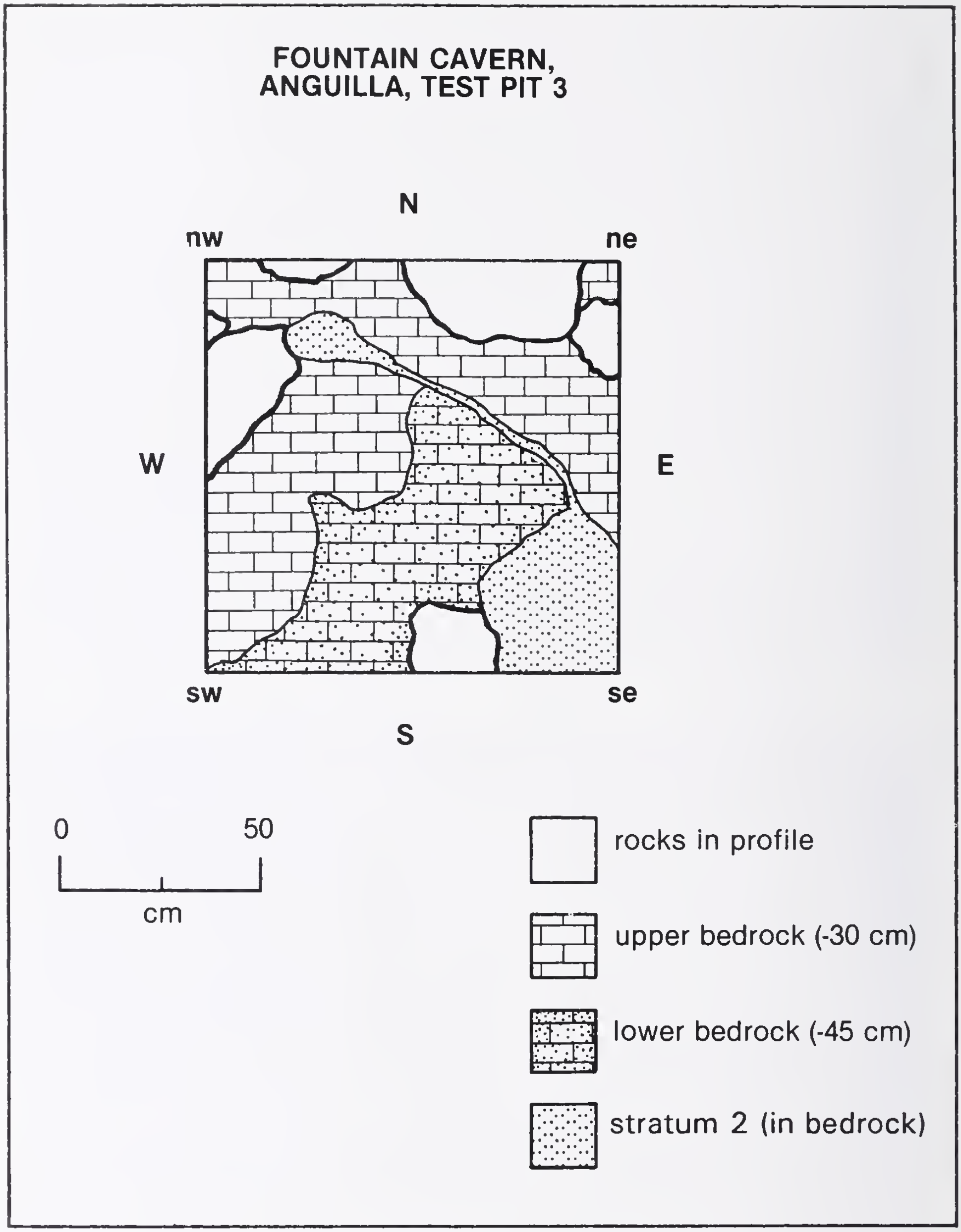


Fig. 16.—Planview of test pit 3 showing different levels of bedrock. Stratum 2 (lacking artifacts) occurred in crevices to a depth of about 75 cm.

The second *Cittarium pica* shell (AL1-RC2) occurred in the southeast profile on the opposite side of test pit 1 from the first shell. It was located 54 cm from the east stake at a depth of 72–75 cm and was the only shell found at that location. The shell yielded a radiocarbon age of 1130 ± 80 years: A.D. 820 (Beta-15486).

Carbon, the preferred material for radiocarbon dating, was absent in test pit 1 with the exception of one small charcoal sample (AL1-RC3) made up of individual pieces collected from the screen and across the test pit at a depth of about 100 cm, by the base of Rock 3 (Fig. 10). AL1-RC3 was given extended counting time (four times normal duration) because of the small amount (0.2 g) of carbon and yielded a radiocarbon age of 1530 ± 140 years: A.D. 420 (Beta-15824).

The radiocarbon ages from these three samples should be viewed with caution for two reasons. The first is the doubtful reliability of cultural association for each sample, despite the fact all three samples were found in proximity to artifacts. The intact *Cittarium pica* shells showed no evidence of alteration by humans, which raises the possibility that they were not deposited in Fountain Cavern by humans. One feasible alternate agent of transport is hermit crabs, which often use empty *C. pica* shells (Randall, 1964:424). A hermit crab falling through the entrance would have been trapped, and the marine shell it inhabited would have remained in Fountain Cavern. Any radiocarbon date derived from a shell introduced by a hermit crab would have no relevance to human use of the cavern. Hermit crabs, including several that carried moderate-sized *Cittarium pica* shells, were seen crawling on the floor beneath the entrance to the cavern during the 1986 fieldwork.

The second reason the ages should be viewed cautiously relates to the kinds and sizes of samples submitted for dating. A date derived from a shell sample is generally regarded as less reliable than a date from a charcoal sample, as the date of death of the mollusk may be two hundred or more years older than the apparent radiocarbon date. The reliability of a radiocarbon age (especially one with a large standard deviation) derived from a small charcoal sample (0.2 g in this instance) is also suspect, particularly when the sample is not a single piece of charcoal but instead is composed of many small individual pieces.

The cultural attribution of the charcoal samples in test pit 1 is more straightforward. It is improbable that a fire from natural causes in Fountain Cavern (which contains few combustible materials) could account for the presence of this charcoal. It is also unlikely that charcoal, produced by an above-ground fire, would subsequently be swept into the cavern and carried to the vicinity of test pit 1. Instead, the charcoal in test pit 1 more logically represents the remnants of a fire or fires resulting from human actions.

At the request of the AAHS, a second radiometric technique, thermoluminescence dating, was tried. Two sherds (AL1-TL1 and AL1-TL2) and associated soil from test pit 1 were submitted to Alpha Analytic, Inc. This dating technique proved to be unsuited for these samples (Alpha-2872 and -2873) because "anomalous fading," induced by volcanic minerals in the sherds, precluded extraction of even minimum ages. The fact the technique proved unsuccessful for the Anguilla sherds is significant because thermoluminescence dating was used to date ceramics in the southern Lesser Antilles (Schvoerer et al., 1985) and elsewhere in the world.

Table 2 summarizes the Fountain Cavern radiometric dating results, none of which inspires much confidence.

ARTIFACTS

Artifacts and miscellaneous materials are segregated into two broad categories: (1) those excavated from test pit 1 (D1-3 through -17), test pit 2 (D1-19), and test pit 3 (D1-20 through -24); and (2) those from the cavern floor surface (D1-1, -2, -25, -26) and from disturbed context in test pit 1 (D1-18, debris from

Table 2.—*Radiometric samples from Fountain Cavern.*

Lab number (Sample number)	Material	Radiocarbon ages*	A.D.	1 Standard deviation
Beta-15485 (AL1-RC1)	shell[a]	1220 ± 70 B.P.	730	660–800
Beta-15486 (AL1-RC2)	shell[a]	1130 ± 80 B.P.	820	740–900
Beta-15824 (AL1-RC3)	carbon[b]	1530 ± 140 B.P.	420	280–560
Alpha-2872 (AL1-TL1)	sherd	unsuited for thermoluminescence dating		
Alpha-2873 (AL1-TL2)	sherd	unsuited for thermoluminescence dating		

* Uncorrected; [a] = *Cittarium pica*; [b] = 0.2 g given extended counting time (4 times normal).

slumped walls) (refer also to Table 1). Excavated artifacts are discussed in three subcategories—prehistoric artifacts, historic and modern artifacts, and miscellaneous material. Individual tables (Tables 3–5) are provided for each excavated subcategory, while surface and disturbed materials are compiled in Table 6. Finally, mollusk remains that were modified into functional objects are treated in the Faunal Remains section.

Prehistoric Artifacts

Excavated prehistoric artifacts include ceramics, lithics, and a three-pointer. They total 779 specimens. Ceramics constitute by far the highest percentage (>98%) of prehistoric artifacts in each test pit (Table 3).

Ceramic

Of a total of 944 prehistoric Amerindian sherds recovered in Fountain Cavern during the 1986 project, 775 (82.1%) were sherds excavated from test pits 1, 2, and 3. Distribution by test pit of the 775 excavated sherds (Table 3) is: test pit 1 (N = 724 or 93.4%), test pit 2 (N = 2 or 0.3%), test pit 3 (N = 49 or 6.3%). All excavated prehistoric sherds were brought to the U.S. for further study but two sherds (one each from D1-4 and D1-8), were sacrificed for the unsuccessful attempt at thermoluminescence dating, leaving 773 excavated sherds for the ceramic analysis. These 773 sherds were combined with seven surface sherds (discussed below, in the section on "Surface and Disturbed Artifacts") to provide a total of 780 prehistoric sherds available for detailed study.

Table 3.—*Excavated prehistoric artifacts at Fountain Cavern, Anguilla.*

Artifact	Test pit 1 (D1-3 to -17)	Test pit 2 (D1-19)	Test pit 3 (D1-20 to -24)	Total
Ceramic	724[a]	2	49	775
Lithic	2	—	1	3
Three-pointer	1	—	—	1
Total ceramic	724 (99.6%)	2 (100.0%)	49 (98.0%)	
Total lithic	2 (0.3%)	— (0.0%)	1 (2.0%)	
Total three-pointer	1 (0.1%)	— (0.0%)	— (0.0%)	
Grand total	727 (100.0%)	2 (100.0%)	50 (100.0%)	779

[a] Two of these sherds were sacrificed for thermoluminescence dating.

A standard vessel lot analysis was conducted using methods derived from prior analyses of North American and Caribbean ceramics (e.g., Petersen, 1980, 1985; Petersen and Power, 1985; Petersen and Watters, 1988). Of the 780 excavated and surface ceramics available for study, 234 (30%) could be assigned to 29 distinct vessels. Data about temper, texture, manufacture, surface finish, vessel morphology, metrics, color and firing attributes, and decoration of these 29 vessels are presented elsewhere (Petersen and Watters, 1991).

Most vessels are spatially segregated in test pits or surface areas (Petersen and Watters, 1991: table 3). Eighteen vessels (3, 5–21) occur solely in test pit 1, seven vessels (22–28) in test pit 3, one vessel (29) in test pit 2, one vessel (1) in Pool 1 (D1-25), and one vessel (2) from Surface Area B (D1-2). Only one vessel (4) occurred in two locations, on the cavern floor (one sherd in Surface Area A) and in nearby test pit 1 (19 sherds).

Although vessels were restricted to individual test pits, in a number of instances sherds from a single vessel were found in different units within a test pit. For example (see Table 1), vessel 5 occurred in five units (D1-3, -4, -5, -10, -11) and vessel 8 occurred in seven units (D1-3, -4, -5, -7, -8, -10, -11) in test pit 1, while vessel 23 was found in three units (D1-21, -22, -23) in test pit 3. Vessel 29, the sole vessel in test pit 2, was represented by only two sherds, both of which were from the same unit (D1-19).

The unit with the most vessels (N = 13) is unit D1-8, located at a depth of 5–35 cm in Sector B of test pit 1, the portion of the test pit where there were no large rocks. D1-8 also had the most sherds (N = 100), although the distribution is biased as 79 sherds are from only three vessels.

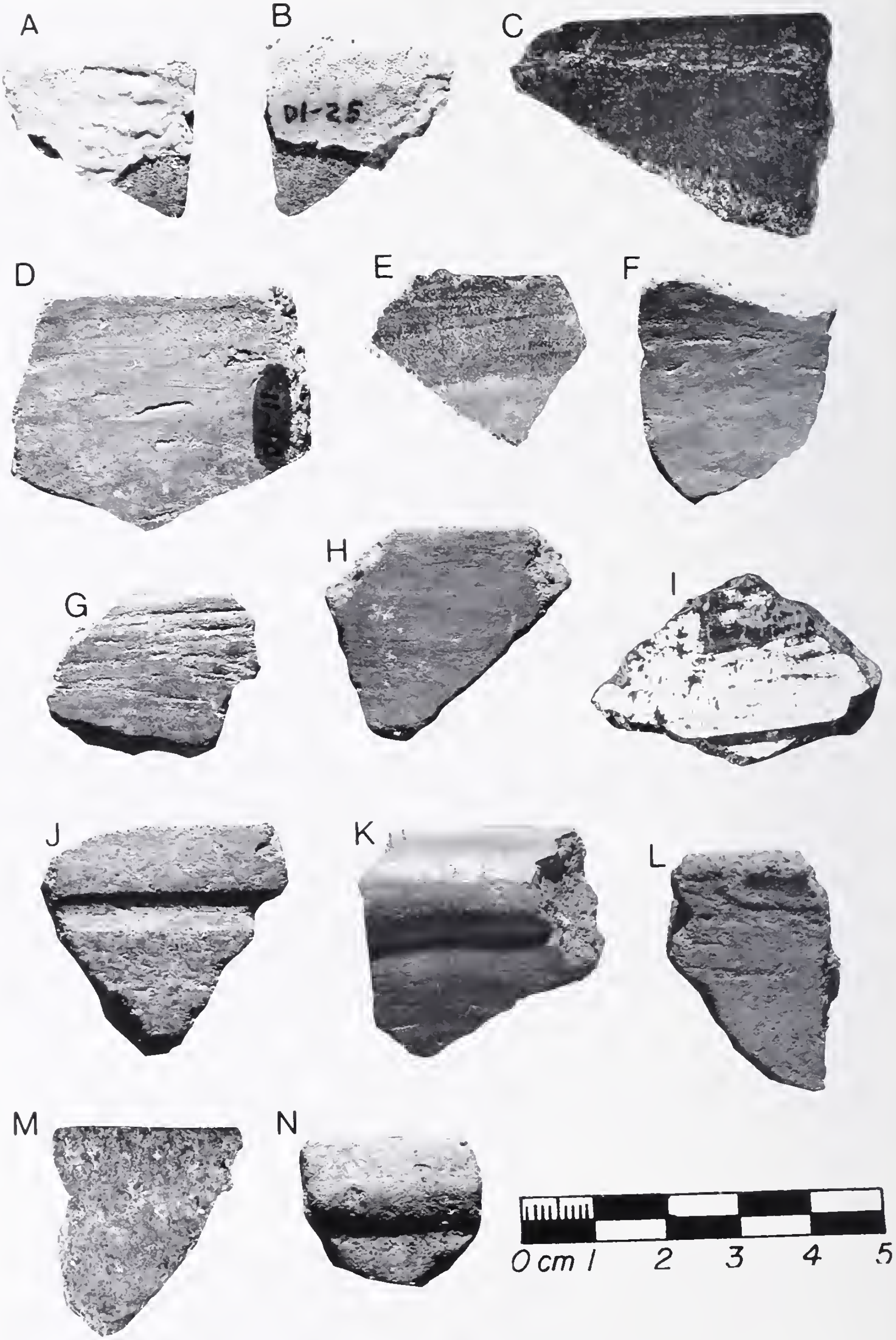
The number of sherds representing each vessel varies widely. Seven vessels include only one sherd each, eight include two sherds, three include three sherds, two include four sherds, one includes five sherds, one includes seven sherds, and one includes eight sherds. At the other extreme, two vessels (75 sherds for vessel 9 and 40 for vessel 8) are very well represented, while four vessels (sherd counts ranging between 11 and 20) are moderately well represented (Petersen and Watters, 1991: table 3).

The vast majority (27 of 29 vessels; 229 of 234 sherds) of the Fountain Cavern ceramics used in the vessel lot analysis exhibit no decoration. They are attributed to the post-Saladoid period. Two vessels exhibit decoration on their exterior surfaces, vessel 17 (four sherds) with white-on-red geometric painting and vessel 19 (one sherd) with a single, deep, U-shaped incision. Sherds from 13 vessels are depicted in Fig. 17 (see Petersen and Watters, 1991: fig. 4–11 for additional photographs of Fountain Cavern ceramics).

Prior to the 1986 project, the AAHS collected prehistoric sherds, first estimated at 5000 to 5500 (Douglas, 1985:11, 1986*b*:28), from the floor of Fountain Cavern. Information on these sherds, all of which remain on Anguilla, is provided in the Discussion section below.

Lithic

Five limestone artifacts, two surface collected (discussed later) and three excavated, were recovered in Fountain Cavern. All surfaces of excavated lithic artifacts are encrusted with a gray layer giving them a uniformly weathered appearance, but beneath that cortex the core of the rock appears gray-green in color. Such limestone reportedly occurs naturally on St. Martin but not on Anguilla.


A
B
D1-25
C
D
E
F
G
H
I
J
K
L
M
N
0 cm 1 2 3 4 5

Limestone artifacts from St. Martin (excavated by Jay Haviser) are visually identical to Fountain Cavern lithics in the cortex and core colors.

Haviser (1988:30) described this stone as gray-green chalky chert but later (Haviser, In press) redesignated it radiolarian limestone. In both diagenetic stages and surface erosion it conforms to the weathered appearance and encrusted layer of the Fountain Cavern lithics. Therefore, the five Fountain Cavern lithics are designated as radiolarian limestone. The limestone from which the artifacts were manufactured, especially in its gray-green core color, definitely differs from the limestone and spall observed in the cavern, thus indicating Fountain Cavern was not the source of the radiolarian limestone. St. Martin is the likely source. The three excavated lithic artifacts are in more advanced states of diagenesis (with thicker encrusted layers) than the two surface-collected objects.

Two radiolarian limestone artifacts were recovered from test pit 1 and a third came from test pit 3 (Table 3). All three are broken, conically shaped (Fig. 18A, B), and of similar size. One test pit 1 artifact (D1-3) is bifacially chipped where one end tapers to an angled edge or ridge (not to a point), while the other end is cleanly broken across the long axis. D1-3 is 54.6 mm long, 36.3 mm wide, 30.3 mm thick, and weighs 81.70 g. The second artifact from test pit 1 (D1-6) has a tapered end which was apparently blunted by pounding. No bifacial flaking was detected on this artifact. The break on the opposite end does not entirely cross the long axis; instead a segment of the rock projects beyond the break. D1-6 has a maximum length (to the end of the projection) of 64.3 mm, a length to the rest of the break of 54.5 mm, a width of 35.7 mm, a thickness of 23.4 mm, and a weight of 69.35 g. The object from test pit 3 (D1-22) is the most heavily encrusted of the three excavated artifacts and its surface alteration (resulting in a friable, almost powdery cortex) seems well advanced. Again, the blunted end shows evidence of pounding but no flaking. The opposite end is broken diagonally across the long axis. D1-22 is 54.0 mm long, 30.4 mm wide, 22.1 mm thick, and weighs 49.77 g.

None of these artifacts seem to match either descriptions or functional categories presented by Haviser (1988, In press) for the St. Martin radiolarian limestone tools. The functions of the Fountain Cavern artifacts remain uncertain, although they may have been used for pounding, grinding, pecking, or otherwise forming the petroglyphs within the cavern. The most heavily encrusted artifact (D1-22) came from test pit 3, where rainfall penetrates through the entrance to the cavern, and its more moist deposits very likely enhanced the physical or chemical alteration of the artifact. For test pit 1 artifacts, D1-6, the most deeply buried artifact (between 30 and 70 cm) is the most heavily encrusted specimen, more so than D1-3, found between the surface and 10 cm, which in turn is more encrusted than the two nearby surface finds. Thus, in the drier part of the cavern near test pit 1,

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←

Fig. 17.—Fountain Cavern prehistoric ceramics. A. Exterior of vessel 1 rim sherd (from cavity near Pool 1) showing the travertine crust. B. Interior of vessel 1 rim sherd. C. Exterior of vessel 5 rim sherd. D. Interior of vessel 8 body sherd. E. Exterior of vessel 9 body sherd. F. Exterior of vessel 10 body sherd. G. Exterior of vessel 11 rim sherd. H. Exterior of vessel 12 rim sherd. I. Exterior of vessel 17 body sherd with white-on-red painting. J. Exterior of vessel 19 rim sherd showing the U-shaped incision. K. Interior of vessel 22 rim sherd. L. Exterior of vessel 23 rim sherd. M. Exterior of vessel 25 rim sherd. N. Interior of vessel 28 rim sherd.

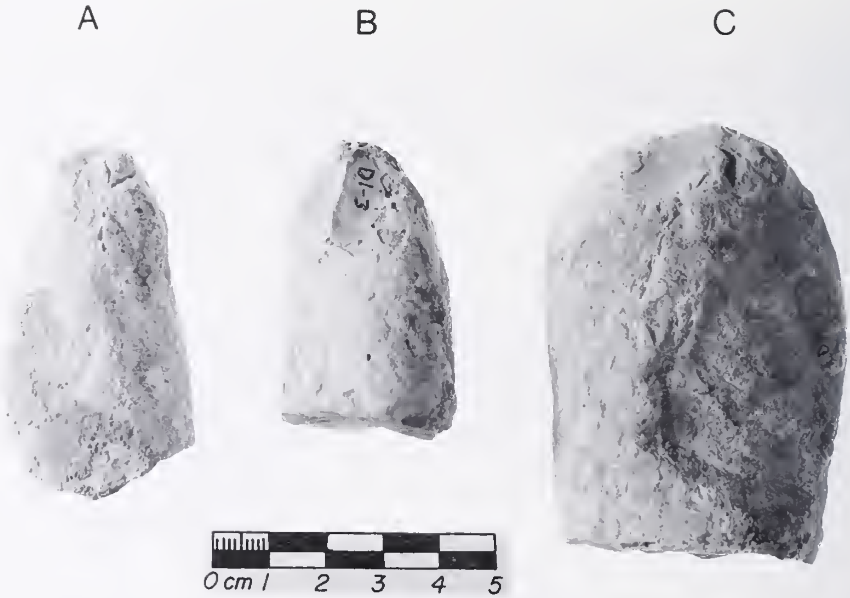

Fig. 18.—Radiolarian limestone tools. A. Blunt-tipped (D1-6) conically-shaped tool excavated from test pit 1. B. Bifacially-chipped (D1-3) conically-shaped tool excavated from test pit 1. C. Bifacial chopper (D1-1) recovered from Surface Area A near test pit 1.

it may be that length of time buried, reflected by depth in the deposit, equates with the degree of diagenesis. The three artifacts have very similar lengths (from tapered tip to the break) at 54.6, 54.5, and 54.0 mm and, being consistently wider than thicker, have elliptical shapes in cross section.

Three-pointer

The final prehistoric artifact is assigned to its own class (Table 3). The three-pointer is made from a marine limestone in which embedded shell fragments are visible. It has the typical triangular shape with the sloping edges joining at the top (Fig. 19). In sideview, the base curves slightly upward to join the lower part of each edge. The base is 37.3 mm long, edges are 33.9 mm and 33.0 mm long, and the height from base to top is 32.3 mm. When the artifact is viewed along an edge, the cross section shows the sides are tapered from the base, the thickest part of the object, to the narrow top, and the base is flattened between the sides. Maximum thickness of the base, measured between the sides across the bottom, is 16.9 mm. Three distinct grooves are incised into the upper part of each edge, between the midway point along the edge and the top (Fig. 19). There are no grooves on the lower portion of an edge. Although they are small, the grooves occur at regular intervals, are consistently U-shaped (not V-shaped) with a slightly rounded bottom, and probably were created by a back and forth "sawing" motion across each edge rather than being cut into the edge as notches. Along one edge the grooves are consistently about 1.1 mm wide and about 1.5 mm deep. Along the other edge, the width varies from 0.9 to 1.7 to 2.4 mm because the wider two grooves encountered natural cavities in the limestone, which in turn caused those two grooves to penetrate deeper. The narrowest groove (0.9 mm) is also the

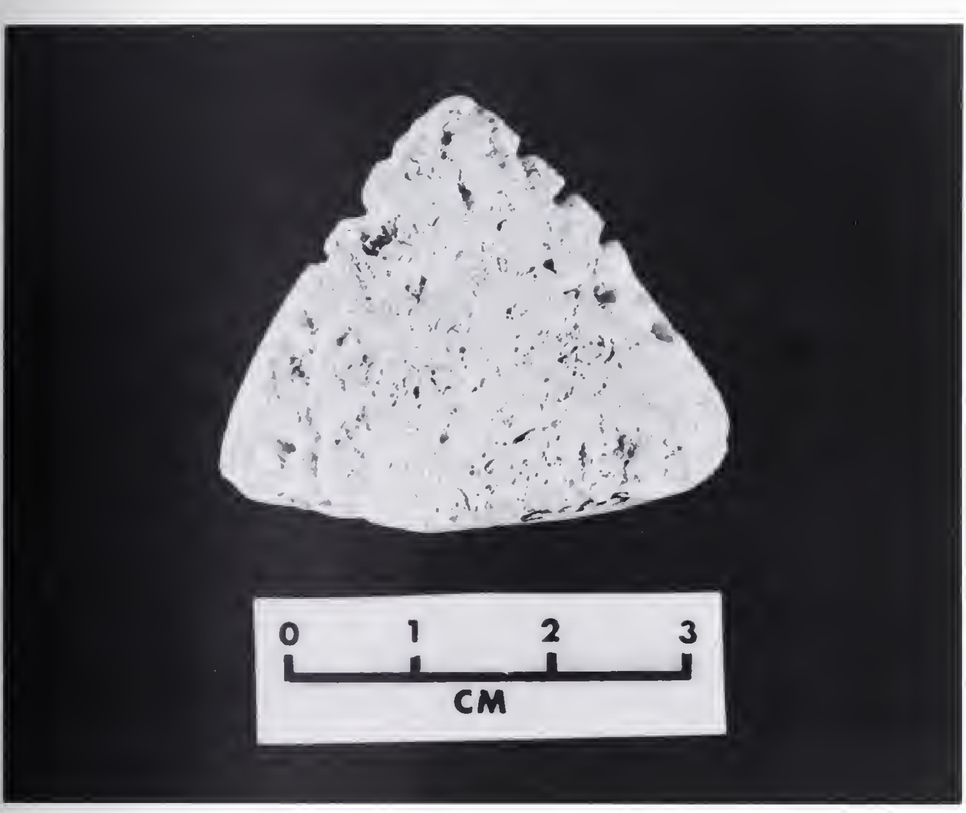

Fig. 19.—Limestone three-pointer ("zemi") showing the set of three grooves incised into each edge.

shallowest. Double sets of grooves have been observed on other Anguillian three-pointers in the care of the AAHS and on three-pointers from Montserrat.

In the West Indies, three-pointers were made of stone, shell, and clay (Rouse, 1986:141). They exhibit considerable variation in size and shape, ranging from small, simple triangular forms, such as the Fountain Cavern specimen, to large, elaborately carved objects incorporating anthropomorphic representations, with the latter being best known from Puerto Rico and the Dominican Republic. Three-pointers are one of several classes of objects subsumed under the term "zemi," and they have long been regarded as objects associated with rituals and ceremonies of "zemiism" (De Hostos, 1923; Fewkes, 1904:178–182, 1907:111–132; Lovén, 1979:578; Rouse, 1986:115, 141). Three-pointer zemis, portrayed as representing ". . . the spirit helpers or supernatural allies of the contact-period chiefs of the Greater Antilles . . ." (Wilson, 1990:19), were highly esteemed objects.

Historic and Modern Artifacts

Excavated historic and modern artifacts from Fountain Cavern are classed as ceramic, glass, plastic, and metal objects. Test pit 1 yielded 43 such artifacts and test pit 3 yielded 46 (Table 4). Fragments of plastic predominated (81.4%) in test pit 1; broken glass (67.4%) did so in test pit 3.

Table 4.—*Excavated historic and modern artifacts at Fountain Cavern, Anguilla.*

Artifact	Test pit 1 (D1-3 to -17)		Test pit 3 (D1-20 to -24)	
	Count	%	Count	%
Ceramic				
Sherds	—	—	3	50.0
Clay pipes	—	—	3	50.0
Total	—	—	6	100.0
Glass				
Old	1	16.7	6	19.4
Clear	1	16.7	15	48.4
Green	1	16.7	4	12.9
Brown	2	33.3	1	3.2
Yellow	—	—	1	3.2
Unspecified	1	16.7	3	9.7
Marble	—	—	1	3.2
Total	6	100.1	31	100.0
Plastic				
White	17	48.6	—	—
Unspecified	13	37.1	—	—
Button	1	2.9	—	—
Flashcube	4	11.4	—	—
Pen cap	—	—	1	100.0
Total	35	100.0	1	100.0
Metal				
Bottle cap	—	—	6	75.0
Pull tab	—	—	1	12.5
Wire	—	—	1	12.5
Coins	2	100.0	—	—
Total	2	100.0	8	100.0
Total ceramics	—	—	6	13.0
Total glass	6	14.0	31	67.4
Total plastic	35	81.4	1	2.2
Total metal	2	4.7	8	17.4
Grand total	43	100.1	46	100.0

Ceramic

Six historic ceramics were recovered at test pit 3. Three are mottled brown stoneware sherds, none of which conjoin although they probably are from the same vessel (Fig. 20). The paste near the interior is cream colored but has a pink cast toward the exterior of each sherd. Sherd thickness ranges from 7.5 to 10.2 mm. One sherd (29.68 g) was recovered from unit D1-22 and two sherds (21.89 and 7.02 g) were recovered from D1-23, the deepest level in test pit 3 located just above bedrock. Such mottled brown sherds are commonly referred to as "Bellarmine" bottles, although that term is inaccurate (Noël Hume, 1969:55). The presence of intermingled historic and prehistoric sherds in the lowest cultural level attests to the disturbed stratigraphy in test pit 3.

The other historic ceramics are pieces of clay (kaolin) tobacco pipes including two bowl fragments and one stem section with the basal part of a bowl. None of these pieces conjoin and there are no maker's marks or other diagnostic impressions. The pipe stem bore diameter is slightly less than $\frac{4}{64}$ in. One bowl fragment

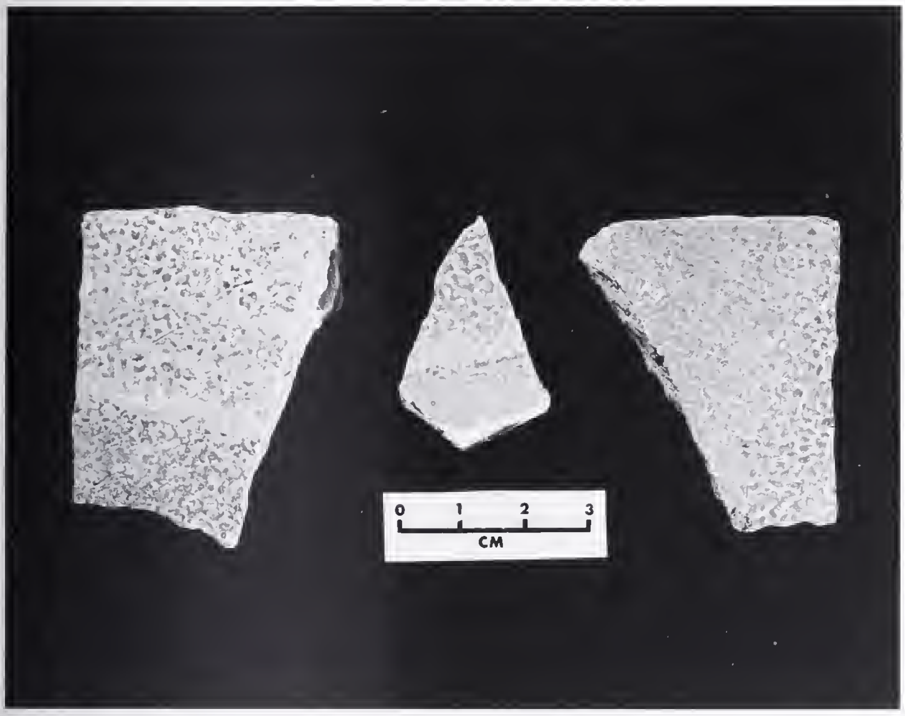

Fig. 20.—Mottled brown stoneware historic sherds from test pit 3. The sherd on the right was recovered in the deepest artifact-bearing level, just above bedrock.

is heavily scorched but the other is minimally charred. All clay pipe fragments came from unit D1-21.

Glass

In Table 4, glass is categorized by color apart from the "old" category, a single broken marble, and the "unspecified" fragments for which color was not recorded. "Old" glass refers to the thick, opaque, dark green to almost black colored bottles of the colonial period that often exhibit patinas and pitted areas because of chemical alteration (Jones, 1986). The rest of the glass fragments are modern in appearance and, apart from the marble, are all bottle parts. In test pit 1, glass fragments were recovered to a depth of 100 cm; in test pit 3 they occurred to 20 cm. Test pit 3 yielded much more glass (N = 31) than test pit 1 (N = 6). Most glass fragments in test pit 3 probably are the remnants of bottles that were dropped or otherwise fell through the entrance and broke on the floor beneath.

Plastic

Bits of plastic were the most abundant modern artifact found in Fountain Cavern. Plastic predominated in the interior of the cavern at test pit 1 (N = 35), where its relative abundance contrasts with its scarcity (N = 1) in test pit 3. The majority were small fragments of plastic containers although one button, a pen cap, and four clear fragments of a photographic flashcube were also recovered. Small pieces of plastic were found as deep as 110 cm in test pit 1. The presence

Table 5.—*Excavated miscellaneous material from Fountain Cavern, Anguilla.*

Material	Test pit 1 (D1-3 to -17)	Test pit 2 (D1-19)	Test pit 3 (D1-20 to -24)	Total
Speleothem	373 (46)[a]	12 (0)[a]	78 (9)[a]	463 (55)[a]
Other material				
Unusual rock	8	—	1	9
Botanical	—	—	1	1
"Fossil wood"	—	—	1	1
Organic	—	—	104	104
Total speleothem	373 (97.9%)	12 (100.0%)	78 (42.2%)	463
Total other material	8 (2.1%)	0 (0.0%)	107 (57.8%)	115
Grand total	381 (100.0%)	12 (100.0%)	185 (100.0%)	578

[a] = Number in parentheses indicates speleothems brought to the U.S. for study.

of flashcube fragments in the dark interior of the cavern is certainly understandable. The plastic container fragments may be remnants of jugs brought to Pool 1 to be filled with water.

Metal

Assorted metal items recovered from test pit 3 included six bottle caps, one beverage container pull tab, and one fragment of rusted wire (Table 4). Two coins were found in test pit 1. One coin, an ECC (Eastern Caribbean Currency) 10-cent piece dated 1981, was recovered near Rock 1 between 35 and 50 cm deep, while another ECC 10-cent coin, dated 1956, was found between 90 and 100 cm. The presence of recent coins at considerable depth in test pit 1 attests to the downward transport of artifacts through crevices among the rocks of Stratum 4.

Miscellaneous Material

The Miscellaneous Material category has two subcategories, "Speleothems" and "Other Material." Excavated Miscellaneous Material is tabulated in Table 5.

Speleothems

The term speleothems refers to massive and crystalline cave deposits, pieces of which were recovered from the floor and test pits in Fountain Cavern. All are composed of calcium carbonate ($CaCO_3$) and most are of a chemical precipitate origin, including fragmented stalagmites, stalactites, flowstone, and dripstone. A few pieces of limestone bedrock are included although they are not actually speleothems. Speleothem fragments probably spalled from the cavern ceiling, walls, and floor during earthquake episodes. They range in size from tiny pieces to the large rocks found in test pit 1 (Fig. 10).

During initial excavation in the uppermost part of test pit 1, all speleothems were collected and examined for evidence of carving or other human modification, as might be expected given the presence of petroglyphs within Fountain Cavern. However, not long after excavation began, the practice of collecting all speleothems was abandoned for three reasons: (1) the quantity of recovered speleothems increased greatly, (2) some were too large (e.g., Rocks 1–4 in test pit 1) to retain, and (3) none displayed cultural modification. Thereafter only selected speleothems from each excavation unit were retained. An effort was made to keep examples of each kind of speleothem from each excavation unit. A second level of selection bias resulted from the decision to limit the number of speleothem specimens that would be brought to the U.S. for further study. The decisions to change collection strategy and to selectively retain specimens were justified on the basis that the pieces occurred naturally and were not really artifacts since none exhibited human modification. Excavated speleothems left on Anguilla (N = 408) are in the care of the AAHS.

Of 463 specimens selectively retained from the Fountain Cavern test pits, 55 (11.9%; 46 from test pit 1, and 9 from test pit 3) were brought to the U.S. for study. Acid (10% HCl) and hardness (Moh's scale of 3) tests and a microscope were used to confirm the presence of calcite, travertine, and limestone in the sample. Medium to coarse crystalline and microcrystalline (micrite) forms were identified as well as a crystal group in one instance; they range from opaque through translucent to transparent. All forms occur naturally in Fountain Cavern.

Some speleothem fragments initially were thought to be culturally modified. These translucent and transparent specimens had flat surfaces (Fig. 21A), abraded surfaces (Fig. 21B), or longitudinal holes (Fig. 22), which resembled respectively purposeful breakage, polishing, or drilling. However, once the specimens were cleaned, it became evident that these features were natural rather than cultural manifestations. Subsequently, it was determined that the flat surfaces are cleavage breaks typical of calcite, the abraded surfaces result from solution etching, and specimens with longitudinal holes are stalactitic forms including a thin-walled variant sometimes called a "soda straw" (Fig. 22). Although these speleothem specimens occur naturally, in form they resemble and could be mistaken for some prehistoric stone artifacts found in West Indies sites, especially beads made from a variety of lithic materials. Calcite crystals (Fig. 23) also were observed in a small cavity exposed just below the surface of a bulldozed track on Anguilla's north coast.

Other Material

"Other Material" includes excavated items not studied in detail and only provisionally classed. None exhibits evidence of human alteration.

Nine red, white, or brown rocks, which may not be natural occurrences in Fountain Cavern or on Anguilla, are classed as "unusual rocks" (Table 5). They were left on Anguilla and have not been studied further.

A single botanical specimen from the lowest level (D1-24) of test pit 3 is an amorphous mass measuring about 2 cm in diameter. The specimen's exterior is a dull brown and its interior consists largely of a translucent, amber-colored material that is probably plant resin, perhaps from the *Clusia* tree at the cavern entrance above the test pit. Without appropriate comparative material, that remains conjectural.

One specimen, a fragment recovered from test pit 3 (D1-22), has been difficult to classify. It has definite cellular structure and seems to be partly mineralized but is lightweight with low density. Initially it was incorrectly identified as stony coral. Further study determined it is porous wood, with incomplete replacement or permineralization by $CaCO_3$. Growth rings are visible in cross section.

A group of soft and friable specimens are labeled simply as "organics" since they have not been identified more accurately. The specimens have powdery surfaces suggestive of weathering and have been attributed to bones, calcareous organic tubes, possibly from worms or clams, or even stalactites by various persons. All specimens were restricted to test pit 3, with the majority (90 of 104

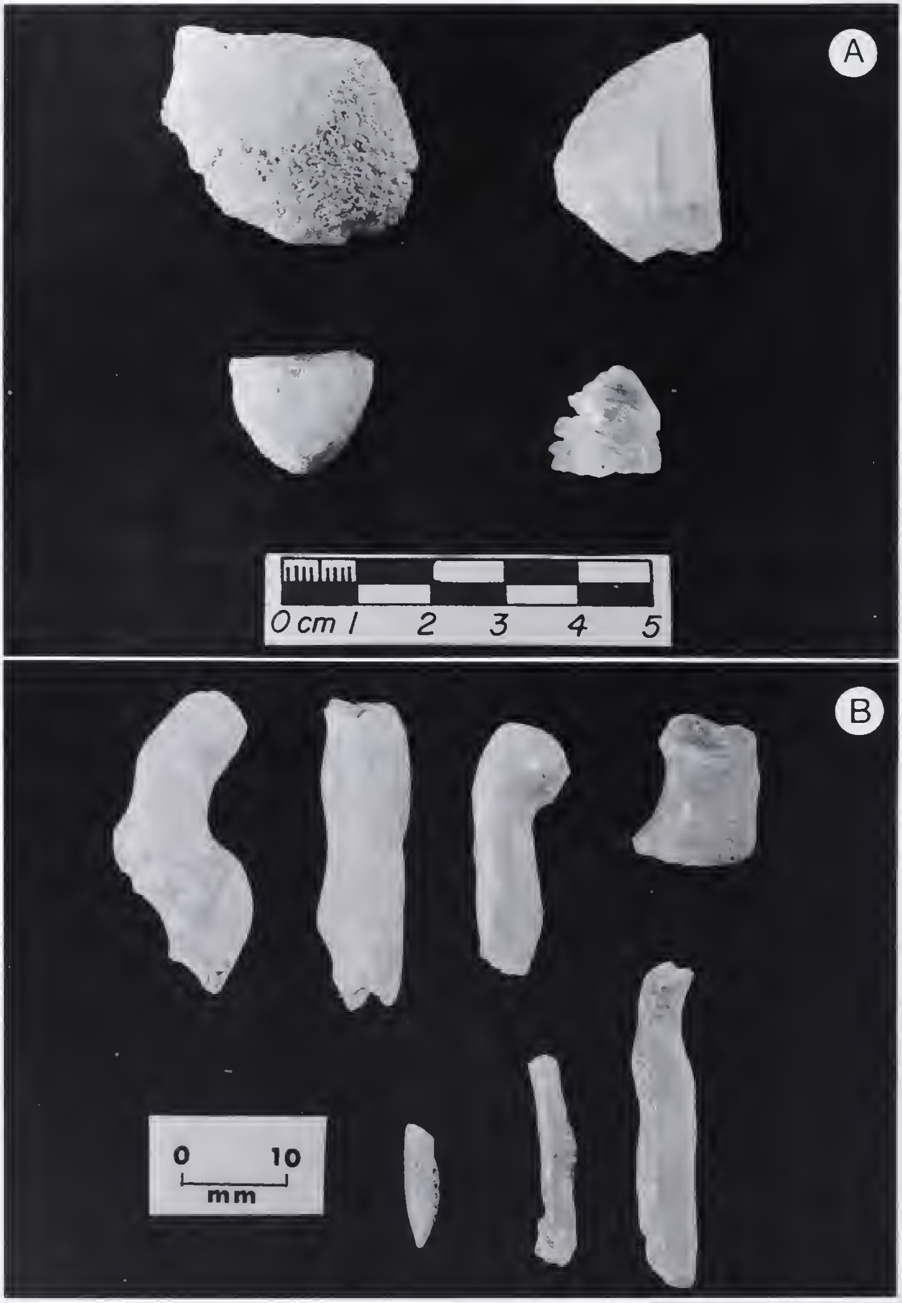

Fig. 21.—Fountain Cavern speleothems. A. Three calcite specimens exhibiting flat cleavage planes and one specimen (lower right) with a small group of crystals. B. Seven translucent and solid crystalline limestone specimens.

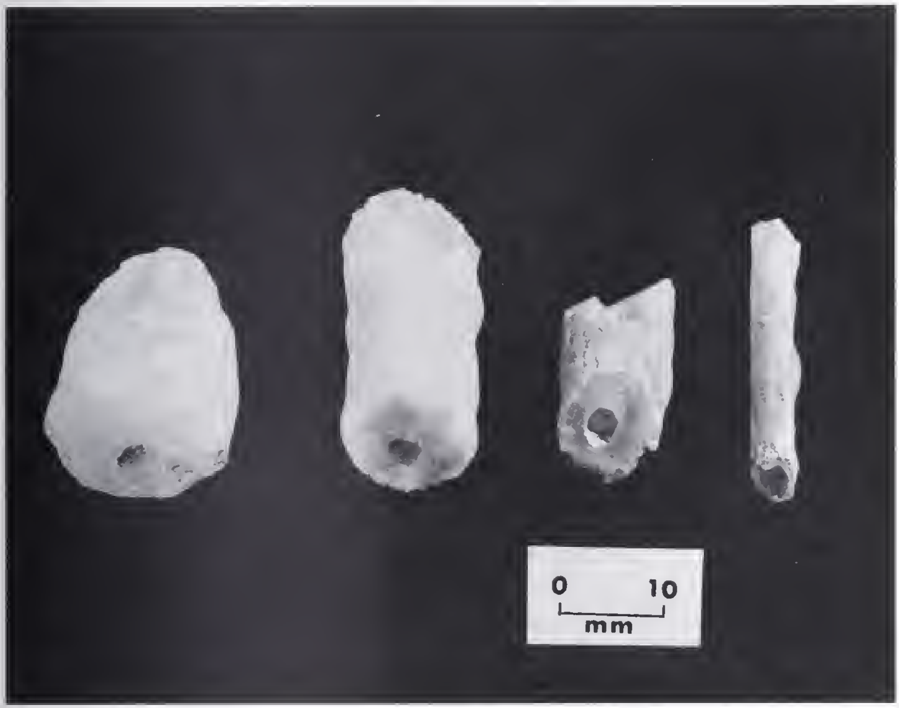

Fig. 22.—Four cylindrical speleothems exhibiting longitudinal holes. These natural specimens resemble and could be confused with unfinished lithic beads. The specimen on the right is typical of "soda straw" stalactites.

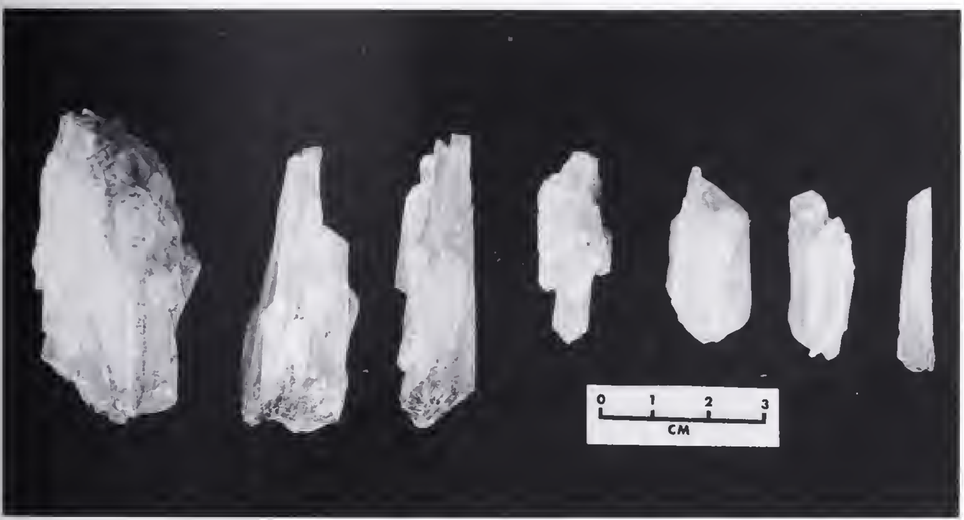

Fig. 23.—Seven calcite specimens found in a non-cave context, a cavity exposed on the surface of a bulldozed road on Anguilla's north coast.

Table 6.—*Surface and disturbed artifacts and miscellaneous material from Fountain Cavern, Anguilla.*

	Surface Area A (D1-1)	Surface Area B (D1-2)	Test pit 1 (slump) (D1-18)	Pool 1 (D1-25)	Petroglyph (D1-26)
Prehistoric					
Sherds	37	20	111	1	—
Lithics	2	—	—	—	—
Historic and modern					
Glass	3	2	3	—	—
Plastic	1	—	8	—	—
Coins	3	—	1	—	—
Miscellaneous					
Speleothem	31 (1)[a]	1 (1)[a]	101 (2)[a]	—	2 (2)[a]
Other material					
Crust[b]	—	—	—	2	—
Unusual rock	3	—	—	—	—
Wood	3	—	—	—	—
Total prehistoric	39	20	111	1	—
Total historic/modern	7	2	12	—	—
Total miscellaneous	37	1	101	2	2
Grand total	83	23	236	3	2

[a] = Number in parentheses indicates speleothems brought to the U.S. for study; [b] = Calcium carbonate (travertine) deposits separated from sherds.

specimens) from D-24, the bedrock fissures where Stratum 2 was present but artifacts were absent. These specimens most likely were deposited before humans began to use Fountain Cavern.

Surface and Disturbed Artifacts and Materials

All artifacts and other materials found on the cavern floor (D1-1, Surface Area A; D1-2, Surface Area B; D1-25, Pool 1; and D1-26, petroglyph rock chip) and in disturbed context in test pit 1 (D1-18, debris from slumped walls) are included in this section and tabulated together (Table 6).

Prehistoric sherds from surface and disturbed contexts total 169 specimens distributed as follows: 37 from D1-1, 20 from D1-2, 111 from D1-18, and one from D1-25. They constitute 17.9% of the 944 sherds recovered at Fountain Cavern. Seven surface sherds (four from D1-1, two from D1-2, one from D1-25) were brought to the U.S.; four were attributable to specific vessels, two of which (vessels 1 and 2) were defined solely from these surface sherds, while one (vessel 4) matched sherds from test pit 1.

An unusual case of post-depositional alteration is displayed by sherds collected by AAHS members during the 1986 project from a water-filled cavity by Pool 1 (D1-25). These sherds exhibit a very distinctive calcium carbonate crust that formed as they lay immersed in the water. Of the 146 sherds found by Pool 1, only a single encrusted rim sherd (Fig. 17A, B) was brought to the U.S. for study. Vessel 1 was defined from that sherd alone. Besides the rim sherd, however, two pieces of crust (Fig. 24), which had separated from other sherds, were brought to the U.S. The crusts are microcrystalline banded travertine. Maximum thickness ranges from 1.3 mm for the rim sherd crust to 5.1 mm and 6.6 mm for the separated crusts. In Table 6, the rim sherd is included in the Prehistoric Artifacts

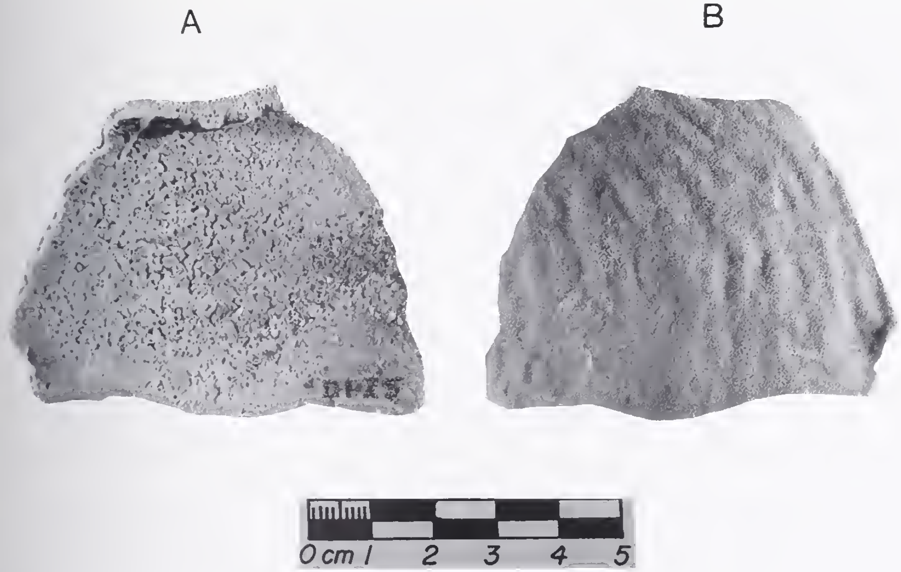

Fig. 24.—Calcium carbonate (travertine) crust deposited on (but now separated from) a rim sherd immersed in Pool 1 (D1-25). A. Interior of crust forming a negative impression of the sherd's exterior surface. B. Crust exterior displaying the wavy depositional pattern. (See also Fig. 17A and B.)

section and the two travertine crusts are tabulated under Miscellaneous Material. The AAHS believes additional vessels are represented among the 145 encrusted sherds remaining on Anguilla.

Two radiolarian limestone artifacts were recovered from Surface Area A (D1-1) near test pit 1. Each artifact has a weathered-appearing cortex, but neither artifact has a cortex as thick as the three limestone artifacts found in test pits 1 and 3. Their cores have the same gray-green color seen in the excavated specimens, but their gray encrusted layers have more brownish hues. The forms of the surface artifacts are decidedly different from the three conically-shaped artifacts recovered from the excavations. The first is the broken end of a celt that was ground to make a curved working edge. The sides of the celt slope inward, to the point where the break occurs, giving the overall impression of a tool that was widest at its base (the working edge) and narrower toward the top. Maximum measurements are a 29.9 mm length from the working edge to the break, a 38.7 mm width of the working edge, a tool thickness of 7.3 mm, and an edge thickness of 2.9 mm; it weighs 9.20 g. The celt is a decidedly thin tool in comparison to other limestone artifacts. The second tool is a large (188.46 g) chopper bifacially chipped on its working edge, both chipped and ground along its sides, and very cleanly broken transversely across its long axis (Fig. 18C). Its measurements are 78.6 mm long, 54.5 mm wide, and 28.6 mm thick. The chopping edge has a maximum thickness of 8.3 mm.

Historic and modern artifacts (Table 6) include eight glass fragments (two brown, three old, three unspecified), nine plastic fragments (all unspecified), and four modern coins. Three coins from Surface Area A (D1-1), adjacent to petroglyph #12 and near test pit 1, are two ECC 25-cent pieces dated 1965 and 1981 and one U.S. 25-cent coin dated 1967; the coin found in slumped wall debris from test pit 1 (D1-18) is an ECC dollar coin dated 1981. No historic ceramic sherds or clay pipes were recovered from the cavern floor or disturbed context.

A total of 135 speleothems was recovered from the cavern floor and slumped walls of test pit 1. These materials are the same as speleothem specimens from excavated context. Six were brought to the U.S. including two small pieces that had broken off the rock on which petroglyphs 1–4 are carved.

Three unusual rocks, two white and one red, were found in Surface Area A (D1-1). They closely resemble the unusual rocks found in the test pits.

Three pieces of wood from tree branches were recovered from Surface Area A on the floor of the cavern near test pit 1. One piece of wood has a charred end indicating it was used as a torch.

FAUNAL REMAINS

Faunal remains from Fountain Cavern include marine and terrestrial invertebrate and vertebrate species. In the *Material* portion of each species account, relevant test pits and provenience codes (D1-3 through D1-17 for test pit 1, D1-19 for test pit 2, and D1-20 through D1-24 for test pit 3) for excavated materials are included. Sections on Surface (D1-1, D1-2) and Disturbed (D1-18) faunas follow the excavated remains in each *Material* list. Only excavated faunal remains are used for estimating minimum numbers of individuals (MNI) for each test pit.

Corals

Two coral specimens representing one species were found in Fountain Cavern. These specimens most likely were deposited in Fountain Cavern by humans. The possibility that they naturally eroded from surrounding limestone cannot be discounted, yet the fact that neither specimen displays marked diagenesis argues against any significant antiquity for the specimens. Corals were matched to identified archaeological samples and by reference to Smith (1971) and Kaplan (1982). The sole excavated coral remain is tabulated in Table 7; it does not count toward MNI because of its fragmentary condition.

Class Anthozoa
Order Scleractinia
Acropora cervicornis (Lamarck, 1816)
Staghorn Coral

Material.—**Test pit 3**: D1-22, fragment; MNI = 0. **Surface**: D1-1, fragment.

Remarks.—Both specimens are fragments of the cylindrical branches that are characteristic of this species. The excavated specimen (D1-22) is heavily worn while the surface specimen retains its tubular cups. *Acropora cervicornis* is a shallow-water species usually found to a depth of approximately 10 m and it is often associated with *Acropora palmata,* the Elkhorn coral. Staghorn and Elkhorn corals are recovered with regularity from Caribbean prehistoric sites.

Sea Urchins

The single sea urchin remain was not identifiable beyond the level of class and is not counted toward MNI.

Table 7.—*Excavated corals, sea urchins, crabs, land snails, and fossil mollusks from Fountain Cavern, Anguilla.*

	Test pit 1 (D1-3 to -17)				Test pit 3 (D1-20 to -24)			
Taxa	Count	%	MNI	%	Count	%	MNI	%
Corals								
Acropora cervicornis	—	—	—	—	1	100.0	0	—
Total	—	—	—	—	1	100.0	0	—
Sea urchins								
Echinoidea sp.	—	—	—	—	1	100.0	0	—
Total	—	—	—	—	1	100.0	0	—
Crabs								
Decapoda sp.	7	100.0	1	100.0	8	100.0	1	100.0
Total	7	100.0	1	100.0	8	100.0	1	100.0
Land snails								
Bulimulus guadalupensis	—	—	—	—	105	45.7	45	30.0
cf. *Macroceramus*	—	—	—	—	1	0.4	1	0.7
Choanopoma sp.	—	—	—	—	124	53.9	104	69.3
Total	—	—	—	—	230	100.0	150	100.0
Fossil mollusks								
Orthaulax aguadillensis	—	—	—	—	4	80.0	0	—
Lucina domingensis	—	—	—	—	1	20.0	1	100.0
Total	—	—	—	—	5	100.0	1	100.0
Total corals	—	—	—	—	1	0.4	0	—
Total sea urchins	—	—	—	—	1	0.4	0	—
Total crabs	7	100.0	1	100.0	8	3.3	1	0.7
Total land snails	—	—	—	—	230	93.9	150	98.7
Total fossils	—	—	—	—	5	2.0	1	0.7
Grand total	7	100.0	1	100.0	245	100.0	152	100.1

Class Echinoidea
Echinoidea sp.

Material.—**Test pit 3**: D1-23, spine; MNI = 0.

Remarks.—The specimen consists of the basal section of a single sea urchin spine.

Crabs

A few crab remains were recovered from test pits 1 and 3. Broken segments of legs predominate, although other exoskeleton fragments also are present. An MNI of 1 has been assigned for each test pit on the basis of the presence of legs.

Class Crustacea
Order Decapoda
Decapoda sp.

Material.—**Test pit 1**: D1-8, leg; D1-13, 2 legs; D1-14, leg, 3 fragments; MNI = 1. **Test pit 3**: D1-22, 2 legs; D1-23, 2 legs, 4 fragments; MNI = 1. **Disturbed**: D1-18, 2 fragments.

Remarks.—The fragmentary remains could not be identified below the order Decapoda. Some specimens may represent the remains of one or more taxa of hermit crabs trapped in Fountain Cavern in the past, much like the living hermit crabs inhabiting mollusk shells that were observed crawling on the cavern floor beneath the entrance during the fieldwork.

Mollusks

Mollusks constitute by far the greatest proportion of faunal remains found at Fountain Cavern. However, the faunal assemblage is biased by the extreme representation of land snails. Land snails can be incorporated into archaeological deposits on an "accidental" basis, as a result of their attraction to refuse concentrated at such sites (Watters, 1989*b*:158); thus the land snail fauna has been treated separately from marine mollusks.

Land Snails

Although they are taxonomically distinct, both terrestrial prosobranchs and pulmonates have been included under the category "Land Snails" in this article. They are tabulated in Table 7.

Land snails were recovered only from test pit 3, the test pit located by the roots of the *Clusia* tree extending downward from the cavern's entrance. This part of Fountain Cavern may be the only area capable of sustaining land snail populations. Most land snails came from unit D1-23 at 20–30 cm, the level immediately above bedrock in which few artifacts were recovered. This suggests many land snails were deposited in the sediments before humans made use of the cavern.

Although MNI for land snails is included, such tabulation does not imply that we regard them as being deposited in the sediments as the direct result of human actions. The MNI is based on apertures because they tend to be better preserved than the thin-walled shells. Fragments refer to broken shells lacking complete apertures.

Class Gastropoda
Subclass Pulmonata
Family Bulimulidae
Bulimulus guadalupensis (Bruguière, 1789)

Material.—**Test pit 3**: D1-21, 6 apertures, 4 fragments; D1-22, 14 apertures, 12 fragments; D1-23, 24 apertures, 41 fragments; D1-24, aperture, 3 fragments; MNI = 45.

Remarks.—*Bulimulus guadalupensis* is a highly variable species in form and color and is widely distributed in the Greater and Lesser Antilles. Breure (1974: table 17) recorded *B. guadalupensis* from Anguilla and *B. guadalupensis* and *B. lehmanni* from Dog Island.

Family Urocoptidae
cf. *Macroceramus signatus* (Guilding, 1828)

Material.—**Test pit 3**: D1-23, aperture; MNI = 1.

Remarks.—This specimen was recovered just above bedrock in test pit 3, the same level that yielded numerous *Bulimulus* and *Choanopoma* specimens. As this is an immature specimen with a missing apical whorl and incomplete last whorl, it is referred tentatively to *Macroceramus signatus.* The species was recorded for Anguilla more than a century ago (Bland, 1861:25).

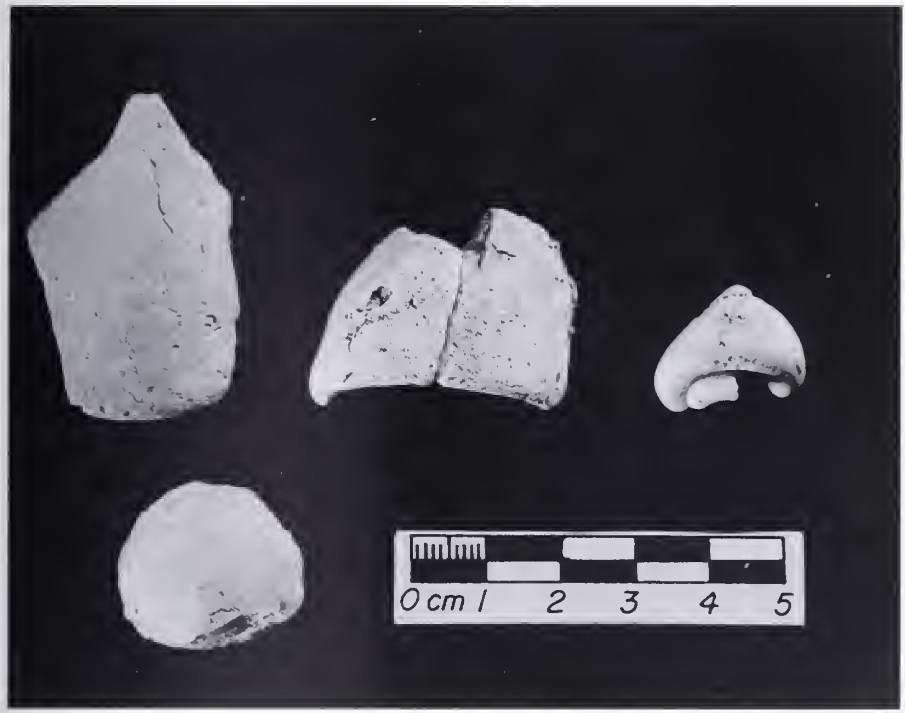

Fig. 25.—Fossil mollusks *Orthaulax aguadillensis* (top row) and *Lucina domingensis* (bottom) from test pit 3.

Subclass Prosobranchia
Family Chondropomidae
Choanopoma sp.

Material.—**Test pit 3**: D1-21, 5 apertures, fragment; D1-22, 15 apertures; D1-23, 76 apertures, 19 fragments; D1-24, 8 apertures; MNI = 104.

Remarks.—The Chondropomidae is an extremely diverse family of Neotropical prosobranchs. *Choanopoma* sp. shells are rugose and thicker and stronger than *Bulimulus guadalupensis,* which accounts for the fact that 69.3% (104 of 124 specimens) of the former retain complete apertures (often as intact specimens) while only 30.0% (45 of 105) of the latter do so (Table 7).

Fossil Mollusks

Five fossil mollusks were found in test pit 3 (Table 7). Although the specimens might have been gathered by humans and deposited by them in test pit 3 along with other faunal remains and artifacts, the fossils also could have been deposited naturally after they eroded from the nearby limestone ceiling or walls.

Family Strombidae
Orthaulax aguadillensis Maury, 1920

Material.—**Test pit 3**: D1-21, cast fragment; D1-22, 2 cast fragments; D1-23, cast fragment; MNI = 0.

Remarks.—The four specimens (Fig. 25) are fragmentary casts of juveniles of

Table 8.—*Excavated marine mollusks from Fountain Cavern, Anguilla.*

Taxa	Test pit 1 (D1-3 to -17)				Test pit 3 (D1-20 to -24)			
	Count	%	MNI	%	Count	%	MNI	%
Gastropoda								
Cittarium pica	222	96.5	17	94.4	74	85.1	10	58.8
Astraea caelata	—	—	—	—	1	1.1	1	5.9
Nerita versicolor	1	0.4	1	5.6	1	1.1	1	5.9
Nerita tessellata	—	—	—	—	3	3.4	3	17.6
Nerita sp.	—	—	—	—	3	3.4	0	—
Tectarius muricatus	—	—	—	—	3	3.4	2	11.8
Serpulorbis sp.	1	0.4	0	—	—	—	—	—
Strombus sp.	4	1.7	0	—	1	1.1	0	—
Cypraea zebra	1	0.4	0	—	—	—	—	—
Oliva sp.	1	0.4	0	—	—	—	—	—
Gastropoda sp.	—	—	—	—	1	1.1	0	—
Total	230	99.8	18	100.0	87	99.7	17	100.0
Polyplacophora								
Acanthopleura granulata	3	100.0	0	—	—	—	—	—
Total	3	100.0	0	—	—	—	—	—
Bivalvia								
Arcinae sp.	—	—	—	—	2	20.0	2	33.3
Lucina pensylvanica	—	—	—	—	5	50.0	3	50.0
Codakia orbicularis	4	100.0	2	100.0	2	20.0	0	—
Chamidae sp.	—	—	—	—	1	10.0	1	16.7
Total	4	100.0	2	100.0	10	100.0	6	100.0
Total gastropods	230	97.0	18	90.0	87	89.7	17	73.9
Total chitons	3	1.3	0	—	—	—	—	—
Total bivalves	4	1.7	2	10.0	10	10.3	6	26.1
Grand total	237	100.0	20	100.0	97	100.0	23	100.0

Orthaulax aguadillensis. Two specimens from D1-22 conjoin. These casts exhibit the characteristic cone-shaped appearance of juvenile *O. aguadillensis,* a common gastropod in late Oligocene to early Miocene (Aquitanian) limestones of the Greater Antilles.

Family Lucinidae

Lucina domingensis (Dall, 1903)

Material.—**Test pit 3**: D1-24, cast; MNI = 1.

Remarks.—This specimen is a complete internal cast (Fig. 25) of *Lucina domingensis,* a common late Oligocene to early Miocene species often associated with *Orthaulax.* It is ancestral to the Recent *Lucina pectinata* (Gmelin, 1791).

Marine Mollusks

Three classes of marine mollusks—gastropods, chitons, and bivalves—were found at Fountain Cavern. Zooarchaeological and Recent collections and malacological sources, including Abbott (1974), Humfrey (1975), and Warmke and Abbott (1975), were used to identify the mollusks. Sequence and nomenclature follow Abbott (1974) except where noted. Marine mollusks are tabulated in Table 8.

Class Gastropoda

With few exceptions, gastropods were identifiable to species despite the fragmented condition of most shells. Whole specimens and broken shells that retained their apices are simply listed as "apices" in the *Material* sections; presence of the apex was the basis of MNI calculations (except for nerites). Fragments are listed separately and were not counted toward MNI.

Family Trochidae
Cittarium pica (Linné, 1758)
West Indian Top-shell

Material.—**Test pit 1**: D1-3, 5 fragments; D1-4, 8 fragments; D1-5, 6 fragments; D1-6, 10 fragments; D1-7, 3 fragments; D1-8, 3 apices, 28 fragments; D1-9, 3 apices, 19 fragments; D1-10, 8 fragments; D1-11, 7 apices, 15 fragments; D1-12, 4 apices, 72 fragments; D1-13, 24 fragments; D1-14, 3 fragments; D1-16, 4 fragments; MNI = 17. **Test pit 3**: D1-20, 3 apices, fragment; D1-21, 2 apices, 24 fragments; D1-22, 5 apices, 21 fragments; D1-23, 17 fragments; D1-24, fragment; MNI = 10. **Surface**: D1-1, 4 apices, fragment. **Disturbed**: D1-18, 4 apices, 100 fragments.

Remarks.—*Cittarium pica* is a monotypic rock-dwelling algae feeder inhabiting primarily the intertidal zone, although larger individuals occur on reefs some distance from shore. It is common in West Indies archaeological sites and constitutes the most abundant taxon in Fountain Cavern (Table 8).

Family Turbinidae
Astraea caelata (Gmelin, 1791)
Carved Star-shell

Material.—**Test pit 3**: D1-21, apex; MNI = 1.

Remarks.—The shell is split in half but one side, complete from apex to aperture, is preserved. The specimen is eroded and most of the spines are worn. *Astraea caelata* inhabits shallow-water rocks.

Family Neritidae
Nerita versicolor Gmelin, 1791
Four-toothed Nerite

Material.—**Test pit 1**: D1-6, aperture; MNI = 1. **Test Pit 3**: D1-22, aperture; MNI = 1.

Nerita tessellata Gmelin, 1791
Tessellate Nerite

Material.—**Test pit 3**: D1-21, aperture; D1-22, aperture; D1-23, aperture; MNI = 3.

Nerita sp.

Material.—**Test pit 3**: D1-22, 2 fragments; D1-23, fragment; MNI = 0.

Remarks.—Nerites are abundant throughout the West Indies on wave-swept rocks facing the open ocean. The limestone cliffs and headlands of Anguilla's north coast, with their numerous crevices and cavities, are ideal habitat for nerites. MNI for nerites is based on presence of the aperture rather than the apex. *Nerita* sp. specimens are fragments of other shell parts and do not count toward MNI. The largest West Indian nerite, *Nerita peloronta,* was absent in the Fountain Cavern materials, which is unusual since it occupies the same habitat as other nerites and commonly occurs in West Indian archaeological sites.

Family Littorinidae
Tectarius muricatus (Linné, 1758)
Beaded Periwinkle

Material.—**Test pit 3**: D1-21, fragment; D1-22, 2 apices; MNI = 2.

Remarks.—Although the Beaded Periwinkle often occurs with nerites on rocky intertidal shores, it also is found above the high-tide line and a considerable distance inland. It is a very common littoral dweller.

Family Vermetidae
Serpulorbis sp.
Worm-shell

Material.—**Test pit 1**: D1-8, fragment; MNI = 0.

Remarks.—The small purplish-brown, coiled specimen may be *Serpulorbis riisei* (Mörch), which Abbott (1974:101) considers possibly synonymous with *S. decussatus* (Gmelin, 1791). The fragment comes from the middle of the shell and does not count toward MNI.

Family Strombidae
Strombus sp.

Material.—**Test pit 1**: D1-6, fragment; D1-8, 2 fragments; D1-9, fragment; MNI = 0. **Test pit 3**: D1-23, fragment; MNI = 0.

Remarks.—All fragments exhibit the lustrous, whitish coloration and denseness that are characteristic of the genus *Strombus.* Two fragments (D1-8 and D1-9) conjoin. Another D1-8 specimen, which consists of a blunt spine with a worn base (Fig. 26A), is similar in appearance to objects that have been argued to be prototypes of three-pointer zemis (Olsen, 1974:36). There are no shell celts among the specimens. None of the conch specimens are used in MNI estimates as they have no apices.

Family Cypraeidae
Cypraea zebra (Linné, 1758)
Measled Cowrie

Material.—**Test pit 1**: D1-13, fragment; MNI = 0.

Remarks.—This specimen, while consisting only of part of the parietal wall and siphonal canal, is of a size that indicates it is an adult *Cypraea zebra.* The species is a moderately common intertidal dweller.

Family Olividae
Oliva sp.

Material.—**Test pit 1**: D1-12, fragment; MNI = 0.

Remarks.—This heavily eroded specimen retains only portions of the parietal wall and outer lip. The apex, columella, and part of the siphonal canal are missing. In general appearance this specimen (Fig. 26B) resembles worked olive shells that are classed as "tinkler" ornaments for necklaces. However, this specimen lacks

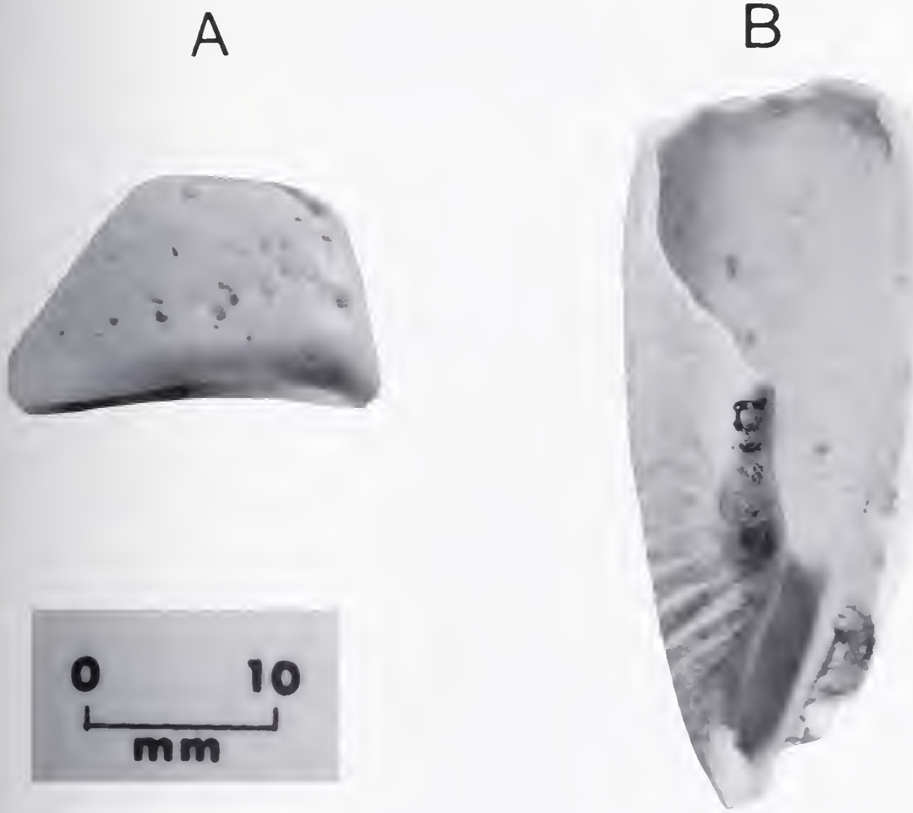

Fig. 26.—Possibly culturally modified shells. A. Heavily worn *Strombus* spine. B. Olive shell resembling a "tinkler" ornament but lacking the usual perforation.

the drilled perforation by which it would be attached to a necklace, that normally characterizes such ornaments. Its size places it within the range of both *Oliva reticularis* and *O. scripta* (termed *O. caribaeenis* by some authors). Olives are nocturnal and carnivorous and inhabit shallow-water sand and mud substrates.

Gastropoda sp.

Material.—**Test pit 3**: D1-22, fragment; MNI = 0.

Remarks.—This fragmentary scrap of shell is undiagnostic and cannot be allocated below the level of class.

Class Polyplacophora

Chiton remains were recovered only from test pit 1. Materials were compared to identified Caribbean chitons found in other archaeological sites. The specimens do not count toward MNI estimates because only median valves, not the singular anterior valve or posterior valve, are present.

Family Chitonidae
Subfamily Acanthopleurinae
Acanthopleura granulata (Gmelin, 1791)
Fuzzy Chiton

Material.—**Test pit 1**: D1-3, median valve; D1-8, median valve; D1-13, median valve; MNI = 0. **Disturbed**: D1-18, median valve.

Remarks.—Median valves of *Acanthopleura granulata* were distinguished by their shape, the presence of blotchy brownish coloration, and the distinctive black splotch on the underside. Although valves generally are eroded, granulated sculpture is observed on all specimens near the girdle margins. Sculpture on one specimen (D1-8) is very well preserved. The species, abundant and widespread in the Caribbean area, inhabits exposed upper intertidal rocks above mean sea level (Glynn, 1970).

Class Bivalvia

Bivalves were much less common than gastropods at Fountain Cavern. MNI is based on presence of left or right beaks, whether from broken or whole valves.

Family Arcidae
Subfamily Arcinae
Arcinae sp.

Material.—**Test pit 3**: D1-21, right valve; D1-23, left valve; MNI = 2.

Remarks.—Although only two valves are present, each represents a different genus. D1-21 has a heavily worn valve margin, but its overall purplish brown color and shape suggest the genus *Barbatia,* more likely *B. cancellaria,* the Red-brown Ark, than *B. domingensis,* the White Miniature Ark. D1-23 has a long, straight hinge line characteristic of *Arca.* As it lacks the zebra-striped markings of *A. zebra,* it more likely is *A. imbricata,* the Mossy Ark. Because both shells are heavily worn, we have chosen to be conservative and retain the subfamily identification. However, both valves count toward MNI. These small shells are juvenile specimens.

Superfamily Lucinacea
Family Lucinidae
Lucina pensylvanica (Linné, 1758)
Pennsylvania Lucina

Material.—**Test pit 3**: D1-21, 3 right valves, 2 left valves; MNI = 3.

Remarks.—Our nomenclature, *Lucina pensylvanica,* for these specimens differs from Abbott (1974:458), who uses *Linga pensylvanica.* The three largest valves are extremely worn and probably were dead specimens collected on the beach.

Codakia orbicularis (Linné, 1758)
Tiger Lucina

Material.—**Test pit 1**: D1-5, left valve; D1-8, right valve, fragment; D1-9, right beak; MNI = 2. **Test pit 3**: D1-21, 2 fragments; MNI = 0. **Surface**: D1-1, right valve. **Disturbed**: D1-18, right valve, fragment.

Remarks.—*Codakia orbicularis* is widespread and abundant throughout the Caribbean. Its range includes much of the tropical western Atlantic where it prefers muddy and sandy substrates in shallow water. *Codakia orbicularis* is a commonplace bivalve in West Indies prehistoric sites.

Table 9.—*Excavated vertebrates from Fountain Cavern, Anguilla. No specimen counts toward MNI.*

Taxa	Test pit 1 (D1-3 to -17) Count	Test pit 2 (D1-19) Count	Test pit 3 (D1-20 to -24) Count	Total
Osteichthyes sp.	1	—	—	1
cf. Teiidae sp.	—	1	—	1
Mammalia sp.	1	—	—	1
Vertebrata sp.	1	—	1	2
Total vertebrates	3	1	1	5

Family Chamidae
Chamidae sp.

Material.—**Test pit 3**: D1-21, left valve; MNI = 1.

Remarks.—This specimen displays some characteristics similar to *Chama macerophylla.* However, because it is small and somewhat worn, we limit our identification to family level.

Vertebrates

The few and very fragmentary vertebrate remains at Fountain Cavern were not counted toward MNI. Excavated vertebrate remains are presented in Table 9.

Class Osteichthyes
Osteichthyes sp.

Material.—**Test pit 1**: D1-13, spine; MNI = 0. **Disturbed**: D1-18, spine.

Remarks.—These undiagnostic fish specimens could not be further identified.

Class Reptilia
Order Squamata
Family cf. Teiidae

Material.—**Test pit 2**: D1-19, metapodial; MNI = 0.

Remarks.—This metapodial, possibly of a ground lizard, was the only faunal remain recovered in test pit 2. Found on the surface and very fresh in appearance, this bone probably is from a recently living lizard and, therefore, has no association with the two prehistoric sherds found in the test pit. It is not counted toward MNI.

Class Aves
Order Charadriiformes
Family Recurvirostridae
Recurvirostridae sp.

Material.—**Disturbed**: D1-18, left distal radius.

Remarks.—This bird bone was recovered from debris that slumped from the sidewall of test pit 1. It is from a member of the stilt family, possibly the Common Stilt, *Himantopus himantopus.*

Class Mammalia
Mammalia sp.

Material.—**Test pit 1**: D1-5, possible right radius fragment; MNI = 0. **Surface**: D1-1, 3 possible right radius fragments.

Remarks.—The three bones were collected previously by the AAHS from the

Table 10.—*Faunal remains from surface and disturbed sectors of Fountain Cavern, Anguilla. No specimen counts toward MNI.*

Taxa	Surface (D1-1)	Disturbed (D1-18)	Total
Anthozoa			
Acropora cervicornis	1	—	1
Decapoda			
Decapoda sp.	—	2	2
Gastropoda			
Cittarium pica	5	104	109
Polyplacophora			
Acanthopleura granulata	—	1	1
Bivalvia			
Codakia orbicularis	1	2	3
Osteichthyes			
Osteichthyes sp.	—	1	1
Aves			
Recurvirostridae sp.	—	1	1
Mammalia			
Mammalia sp.	3	—	3
Total surface/disturbed	10	111	121

surface of the cavern, while the D1-5 fragment was excavated by the author. The bones cross mend and are from the same individual. They seem to be fragments of the radius or, less likely, the ulna. While these limited remains are reminiscent of *Homo sapiens* bones in size and shape, they have hollow medullary areas and thick compact bone layers that are unusual for human bone.

Vertebrata sp.

Material.—**Test pit 1**: D1-8, fragment; MNI = 0. **Test pit 3**: D1-21, fragment; MNI = 0.

Remarks.—These fragmentary scraps of bone are wholly undiagnostic.

Surface and Disturbed Faunal Remains

Faunal remains recovered from Surface Area A (D1-1) and the slumped walls of test pit 1 (D1-18) include coral, crab, marine gastropod, chiton, bivalve, and vertebrate specimens. As these remains were not found in verified archaeological context, their relationship to Amerindian use of Fountain Cavern is equivocal. They are listed in Table 10. All surface and disturbed taxa have counterparts in excavated units with the exception of the single bird bone of the family Recurvirostridae. *Cittarium pica* shells (N = 104) were the most abundant faunal remain from the slumped walls of test pit 1 (D1-18).

Discussion of Faunal Remains

Table 11 presents the counts, MNI, and their percentages for major categories of excavated faunal remains from test pits 1, 2, and 3. Land Snails is the only category excluded from Table 11 because they probably were not deposited by humans in test pit 3, and their extreme representation, 230 of 343 specimens (93.1%) and 150 of 175 individuals (85.7%), in that test pit skews the sample. While it is also unlikely that Amerindians played a role in the deposition of some other faunal categories (e.g., the five fossil shells or Recent lizard bone), we have opted to include them in Table 11 because neither faunal category seriously skews

Table 11.—*Excavated faunal remains by faunal category (excluding land snails).*

	TP1 (D1-3 to -17)				TP2 (D1-19)				TP3 (D1-20 to -24)			
Category	Count	%	MNI	%	Count	%	MNI	%	Count	%	MNI	%
Coral	—	—	—	—	—	—	—	—	1	0.9	0	—
Sea urchin	—	—	—	—	—	—	—	—	1	0.9	0	—
Crab	7	2.8	1	4.8	—	—	—	—	8	7.1	1	4.0
Fossil	—	—	—	—	—	—	—	—	5	4.4	1	4.0
Gastropod	230	93.1	18	85.7	—	—	—	—	87	77.0	17	68.0
Chiton	3	1.2	0	—	—	—	—	—	—	—	—	—
Bivalve	4	1.6	2	9.5	—	—	—	—	10	8.9	6	24.0
Fish	1	0.4	0	—	—	—	—	—	—	—	—	—
Reptile	—	—	—	—	1	100.0	0	—	—	—	—	—
Mammal	1	0.4	0	—	—	—	—	—	—	—	—	—
Vertebrate	1	0.4	0	—	—	—	—	—	1	0.9	0	—
Total faunal	247	99.9	21	100.0	1	100.0	0	—	113	100.1	25	100.0

the data. Finally, one other faunal category that is included, marine gastropods (especially *Cittarium pica*), may involve some whole specimens brought into the cavern by hermit crabs, not by humans. Since intact shells introduced by hermit crabs were not distinguishable from those possibly brought in by humans, all the marine gastropods are tabulated in Table 11.

Of 11 faunal categories included in Table 11, seven occur in test pit 1, one in test pit 2, and seven in test pit 3; only four categories (crab, gastropod, bivalve, unidentified vertebrate) are common to test pits 1 and 3. Test pit 2, with only a single lizard bone, is not considered further.

With regard to counts, test pit 1 (N = 247) has more than twice as many faunal remains as test pit 3 (N = 113). Each test pit has a single faunal category, gastropod (marine), that by count constitutes the bulk of its specimens, with 230 of 247 (93.1%) in test pit 1 and 87 of 113 (77.0%) in test pit 3. All other faunal categories in both test pits have ten or fewer remains (<9.0%) and three categories in each test pit have only one specimen (<1.0%).

In terms of MNI, test pit 3 with 25 exceeds test pit 1 with 21. Again, gastropods predominate, with 17 (68.0%) in test pit 3 and 18 (85.7%) in test pit 1. The gastropod MNIs are similar but percentages of total gastropods are not (18 of 230 or 7.8% for test pit 1; 17 of 87 or 19.5% for test pit 3). Gastropod shells with apices (or apertures in the case of nerites) were found 2.5 times more frequently in test pit 3 than test pit 1. However, Table 8 shows almost all apices in test pit 1 are from *Cittarium pica,* whereas seven apices in test pit 3 are from small gastropods (*Astraea, Nerita,* and *Tectarius*) in addition to ten *C. pica* apices. If only *Cittarium pica* remains are used (Table 8), the MNI as a percentage of total remains changes to 7.7% (17 of 222) for test pit 1 and 13.5% (10 of 74) for test pit 3, which means that *C. pica* apices are found slightly less than two times more frequently in test pit 3. *Cittarium pica* remains are not only more abundant in test pit 1 but also tend to be fragmented and missing more apices. Bivalves also are well represented in test pit 3, with six individuals accounting for 24.0% of total MNI.

The last point about Table 11 concerns the distribution between marine and terrestrial organisms. Even with two categories excluded (fossil marine mollusks and unidentified vertebrates), six of the nine remaining faunal categories are marine (coral, sea urchin, gastropod, chiton, bivalve, fish) and only three are terrestrial (crab, reptile, mammal). Moreover, by count, marine specimens constitute the far greater quantity and percentage (238 of 246 or 96.7% in test pit 1; 99 of 107 or 92.5% of test pit 3), as well as by MNI (20 of 21 or 95.2% for test pit 1; 23 of 24 or 95.8% for test pit 3). Test pit 2, having but a single remain of a recently living lizard, does not constitute a valid sample.

The modern invertebrate and vertebrate faunas of Anguilla are poorly known at this time and thorough faunal studies will be required before definitive statements can be made about possible relationships between modern and past (both paleontological and archaeological) faunas of this island (Watters, 1989*b*). Recent reports are available on Anguilla's gastropods (Coomans, 1958), chitons (Kaas, 1972), land snails (Breure, 1974), bats (Genoways, 1989), tortoise and tree frog (Censky, 1988, 1989), and extinct heptaxodontid rodent *Amblyrhiza inundata* (McFarlane and MacPhee, 1989; cf. Watters, 1989*b*).

PETROGLYPHS

Fountain Cavern was first recognized as a prehistoric site in 1967 after June Flowers discovered its petroglyphs. A survey by the Island Resources Foundation (1980; Dick et al., 1980) in 1979 recovered the first artifacts and confirmed the cavern's status as a prehistoric site. Reports of that survey neither described nor enumerated the petroglyphs in Fountain Cavern.

Since Fountain Cavern's petroglyphs have been illustrated by Penny Slinger as well as presented in manuscript, checklist, and now published form (Douglas, 1985, 1986*a*, 1989), they are only briefly discussed here. All 12 petroglyphs are in Chamber 1. Nine petroglyphs (reference numbers 1–9 in Douglas's lists) are found in close proximity to the north wall and relatively close to the entrance, the sole source of light in the cavern, and one (#10) occurs on the slope. The majority of these carvings are representations of faces or encircled eyes (Fig. 27). The other two petroglyphs are located in the vicinity of Pool 1 about 15 m south of the others. Petroglyph 11, named by Douglas the "Chief" or "Solar Chieftain" (Fig. 28A), faces Pool 1 from the base of the adjacent truncated column. Petroglyph 12, termed "Jocahu" or the "Creator" by Douglas, is a face carved at the pinnacle of the tall stalagmite (Fig. 28B). It was the base of this stalagmite that encroached into and occupied about 50 percent of the area at the deepest part of test pit 1 (Fig. 11). Petroglyph 12, atop the stalagmite, is almost 6 m above the bottom of test pit 1.

The age of the Fountain Cavern petroglyphs remains uncertain since dates are not available for the rock carvings. Almost all Amerindian ceramics recovered during the 1986 research project are undecorated sherds (see the Artifacts section and Petersen and Watters, 1991) that are attributable to a post-Saladoid occupation of Anguilla, which in turn suggests the petroglyphs most likely date to the post-Saladoid time period as well.

Fountain Cavern's petroglyphs were briefly discussed by Petitjean Roget (1989), who stated they were made around A.D. 900, and Dubelaar (1989), who suggested A.D. 1200, both being dates that are in accord with the post-Saladoid attribution of the Fountain Cavern Amerindian ceramics.

DISCUSSION

AAHS Artifacts

Douglas (1985:11, 1986*b*:28) initially estimated 5000 to 5500 prehistoric sherds were collected from Fountain Cavern before the 1986 excavations. A recounting

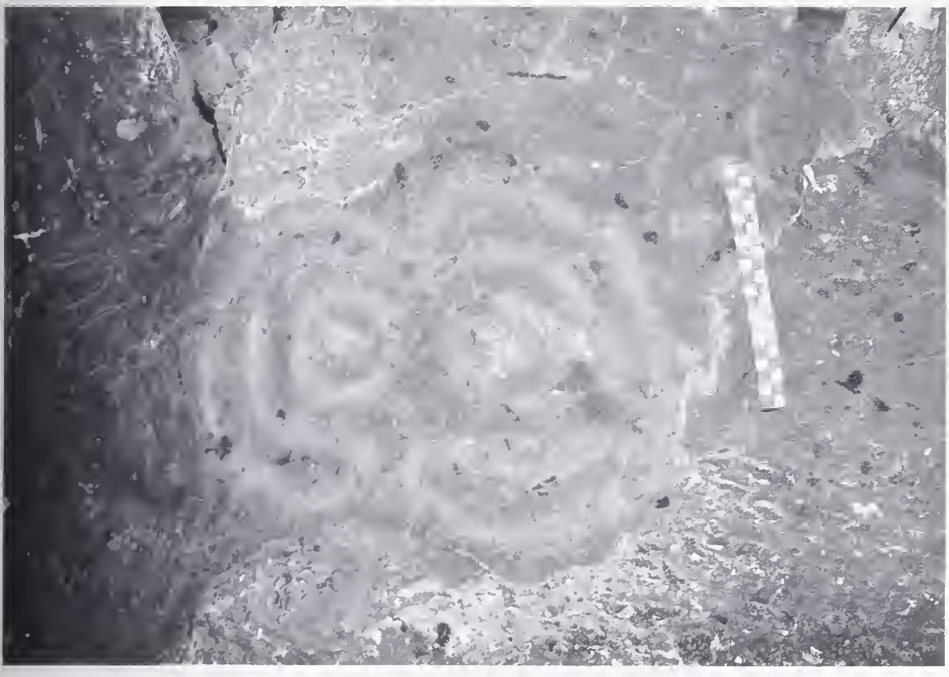

Fig. 27.—Petroglyph 6 displaying loop encircled eyes.

of those materials, combined with additional artifacts collected since the 1986 project, increased the total number of artifacts and faunal remains collected by the AAHS from the floor of Fountain Cavern to 6641. Three are lithic tools, 25 are mollusk shells, nine are historic ceramics, and 6604 are prehistoric sherds. These materials, which remain on Anguilla, have not been studied by the author. Douglas (personal communication, 1991) provided information about the AAHS materials, from which the summary below is extracted.

All materials came from Chamber 1. Of the 6604 prehistoric sherds, ten were found in Pool 1, 145 (encrusted sherds discussed previously) in the water-filled cavity beside that pool, 55 on the floor sloping from the level area beneath the entrance (by the ladder and the nine petroglyphs) toward Pool 1, and 6394 in the vicinity of the large stalagmite (an area roughly equivalent to Watters' Surface Area A) (Fig. 6). Although a grid was not used by the AAHS to collect artifacts in a systematic manner, the distribution pattern shows that prehistoric sherds certainly were concentrated near the stalagmite with Petroglyph 12.

Twenty sherds have some form of decoration on the exterior, including seven with white-on-red painting, one that is a painted spiral-shaped handle, and 12 with modelled decoration including two adornos, one of which may depict a snake and one possibly a snail. Of the remaining 6584 sherds, 650 are too fragmentary or small to ascertain whether or not they were decorated. A total of 5934 sherds exhibit no decoration.

Douglas provided additional information about varieties of bases and rims, vessel shapes, and probable numbers of vessels represented, some of which is included by Petersen and Watters (1991).

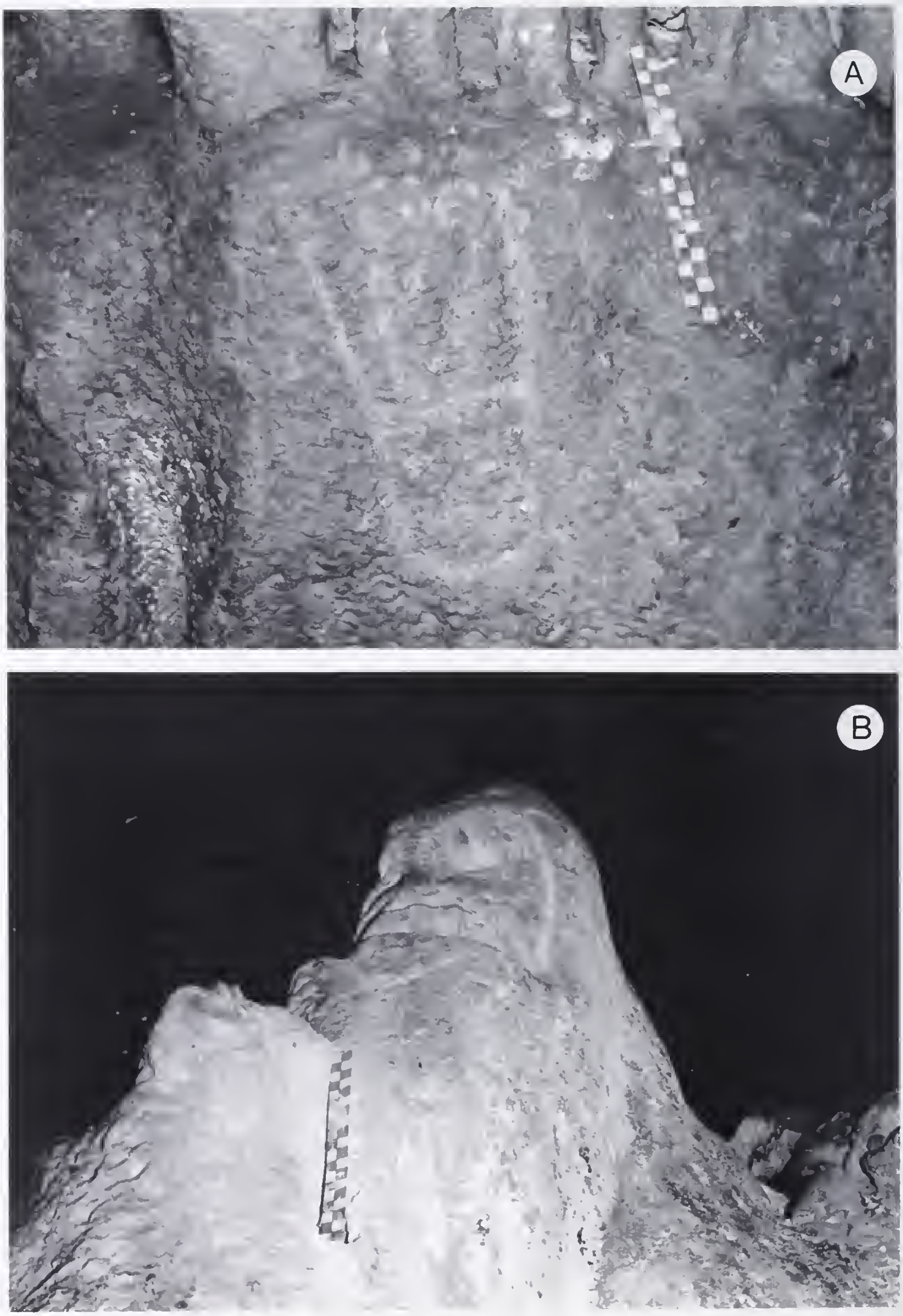

Fig. 28.—A. Petroglyph 11 near the base of the truncated column near Pool 1. B. Petroglyph 12 carved atop the large stalagmite bordering test pit 1.

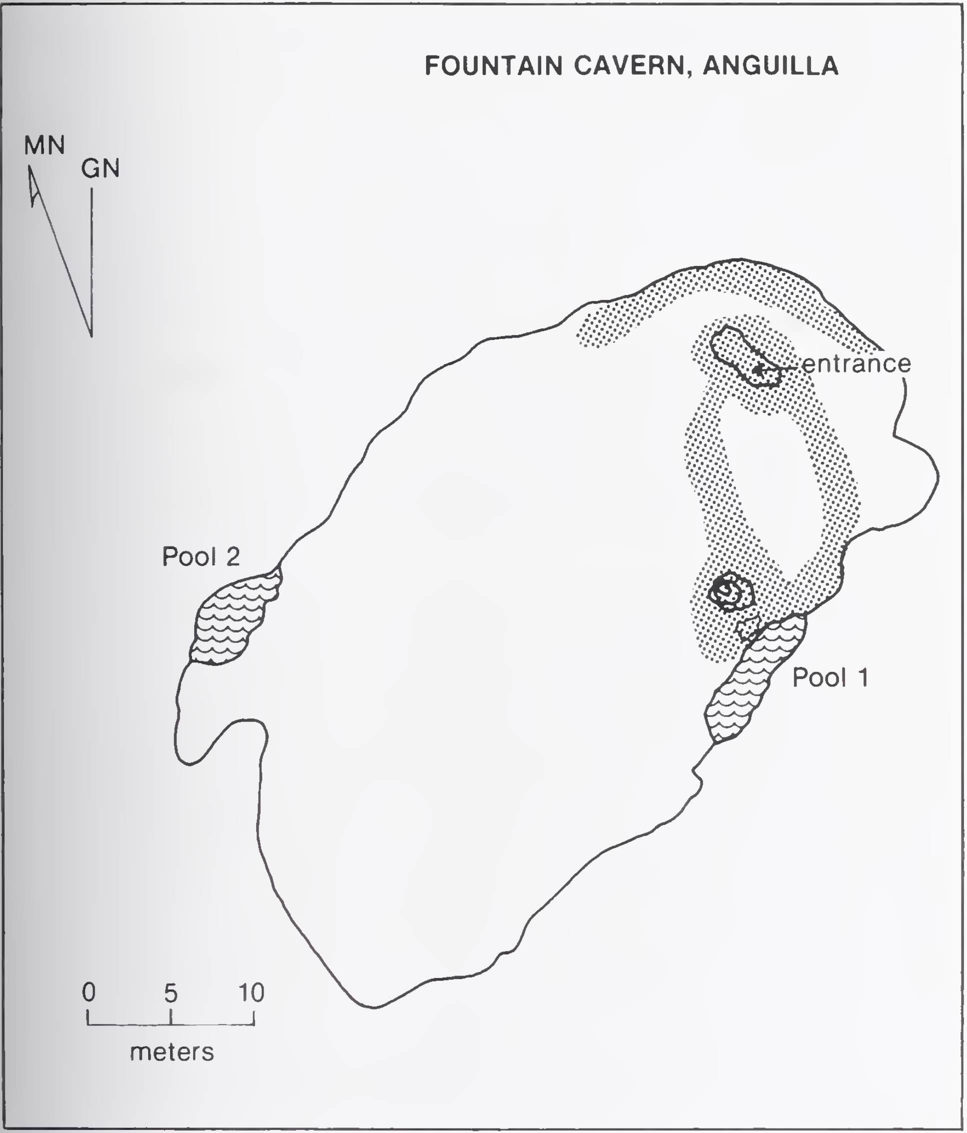

Fig. 29.—High probability areas (stippled) for concentrations of artifacts in Fountain Cavern.

Data Limitations

Although three test pits were excavated in Fountain Cavern during the 1986 project, their combined area (3 m^2) represents a small percentage of the total archaeological deposits. Figure 29 shows the high probability areas for archaeological deposits in Fountain Cavern based on the surface survey, test excavations, and discussion with AAHS members about their earlier surface collecting activities. Certain areas that were not tested and for which information about the depth of the deposits remains unknown, such as the two washes (Fig. 6), should be tested to determine whether they contain prehistoric artifacts. Further excavation in Chamber 2 is not justified in view of its paucity of artifacts and shallow sediment depth, but a more intensive survey of its numerous crevices would be warranted.

Archaeological materials from test pits 1 and 3 cannot be regarded as being in primary context and, therefore, they were not segregated into discrete stratigraphic levels or units for analytical purposes. No distinct cultural strata or levels were discernible in any test pit. Prehistoric, historic, and modern artifacts were intermingled in test pit 1, often at considerable depth. In addition, prehistoric sherds from the same vessel were recovered from different depths in the test pit. Trampling and shifting of rocks by humans probably accelerated the mixing of materials from different time periods. However, there was no indication of humans having purposefully dug up or turned over the deposits, except perhaps in a shallow depression in the north corner (Sector C) of test pit 1. The disturbance in test pit 3 resulted from installation of a steel ladder, during which prehistoric, historic, and modern artifacts were mixed throughout the sediments (except in the bedrock fissures). While test pit 1 was subject to a "passive" taphonomic process, whereby younger artifacts were added to or agglomerated with older materials in place in lower levels, in test pit 3 both the artifacts and the strata were actively churned. In test pit 2, only two partially buried sherds were found in what essentially was the surface level.

In test pit 1, stratigraphic context of cultural materials was affected by two other factors, the intrusion of the base of the stalagmite and the presence of four large rocks (Fig. 10, 11). These impediments meant that uniform 10-cm excavation levels could not be maintained throughout the test pit (Table 1), and vertical control was most difficult between about 50 and 90 cm where Rock 3 interposed. The three largest rocks were stacked against the stalagmite and they penetrated the walls of the test pit, ultimately causing slumping and the disturbed materials from unit D1-18. The deepest large rock, Rock 4, was wedged between the stalagmite base and cavern floor. Only Rock 1 in Sector B (southern half of the test pit) was distant from the stalagmite. Prehistoric artifacts were found adjacent to and beneath all four rocks (although the "deep pit" by Rock 4 yielded few materials), which suggests that the cavern was in use by prehistoric peoples when the rocks came to rest against the stalagmite. The rocks could have fallen or rolled to those positions, perhaps as a consequence of earthquakes. The highest density of artifacts was in Sector B between 5 and 35 cm (D1-8). Sector B was the part of the test pit most distant from the stalagmite, included only the smallest (Rock 1) of the large rocks, and consisted mainly of sediment and cobbles (Fig. 9, 10).

The final limitation involves the three radiocarbon dates, none of which inspires much confidence.

Caves and Petroglyphs

Caves were a recurring element in the mythology of the Taino, the Amerindian group inhabiting most of the Greater Antilles when the Spanish explorers arrived. The significance of caves is known through the work of Ramón Pané, a friar who lived among the Taino for two years in the mid-1490s. Bourne (1906) translated Pané's treatise into English (see Fernández Méndez, 1981:11–32 for a Spanish version). Pané (in Bourne, 1906:319–320) reported a Taino myth in which the larger part of the people (=Taino) to settle the island of Española (=Hispaniola) came forth from a cave named Cacibagiagua led by a man named Guagugiona. Stevens-Arroyo (1988:136–138) interprets this as a Taino hero myth. Pané also recorded the Taino belief that the sun and moon came forth from another cave, which they held in high regard and "painted in their fashion" (in Bourne, 1906: 325). This cave also contained two stone zemis that the Taino visited in times of drought to induce rainfall.

Archaeological research has shown that caves were used as dwellings for habitation only rarely by Amerindian groups in the West Indies. Villages of Ceramic Age Amerindians, who were horticulturalists, typically are located at open sites. Presence of pottery in caves was misinterpreted by some early researchers as evidence of cave-dwelling. Lovén (1979:122), however, refuted that position, arguing that occurrence of pottery remains is not sufficient evidence to document habitation in caves.

Caves were one of three locations used by the Taino to bury their dead (Wilson, 1990:22). Columbus (cited in Bourne, 1906:313) reported that Taino caciques (=chiefs) sometimes were buried in caves. Harrington (1979) recorded many cave burials in Cuba, and Lovén (1979:123–124) argued that caves most often were used as burial places and recorded cases from Jamaica and St. Vincent where the bones had been placed in ceramic burial urns. Lovén (1979:130) argued against differentiating too strongly between Taino burial caves and shrine caves, since the objects of zemiistic worship in caves included the ancestors' bones as well as stone and wooden idols.

Stevens-Arroyo (1988:64, 138) stated that caves, for the Taino, were special places for rites involving hallucinogenic substances and sanctuaries where religious artifacts were reserved for ritual purposes. Lovén (1979:125–130) mentioned artificial niches or platforms for setting images in shrine caves, recovery of artifacts associated with zemiistic rituals in cave-temples, and the presence of petroglyphs and pictographs in various caves in the Greater Antilles. He also cited a historical record of idols being found in a cave on Martinique in the Lesser Antilles.

In Cueva Zemi in eastern Cuba, Harrington (1979:268–273, plates LIX and LX) found a large stalagmite on which was carved a face and indications of a body, in front of which was a blackened earth area about eight feet in diameter with ashes mixed with faunal remains, flint flakes, and plain pottery to a depth of about eight inches. The description of the Cueva Zemi carving closely resembles the Fountain Cavern stalagmite with Petroglyph 12. Lovén (1979:127) referred to the Cueva Zemi specimen as zemiistic sculpture illustrating the transition from petroglyphs to more plastic representation, a characterization paralleled by Dubelaar's (1989:16) contention that the Fountain Cavern specimen is a statue rather than a petroglyph. Anthropomorphic petroglyphs and carved stalagmites also are reported on Hispaniola (Krieger, 1931:21; Veloz Maggiolo, 1972:153, 163).

Petroglyphs sites are widely distributed in the West Indies and are abundant on some islands, such as the Dominican Republic where 72 petroglyph and pictograph sites are recorded (Pagán Perdomo, 1979). Petroglyph sites are not always associated with caves. Lovén (1979:125) argued that since caves occur rarely in the inner, volcanic arc of the Lesser Antilles because the volcanic deposits were not suited for cave development, petroglyphs on these volcanic islands are located on the surface, especially on rocks near streams and rivers. The Layou site on St. Vincent (Kirby, 1970) typifies surface sites. However, caves are prevalent on the limestone islands of the outer arc in the Lesser Antilles, and they provide suitable settings for subterranean petroglyphs. Therefore, although Fountain Cavern, with its abundant subterranean petroglyphs, is regarded as a rare site type in the Lesser Antilles, similar subterranean petroglyph sites occur in cavernous areas of islands in the Greater Antilles. Anguilla's nearest neighboring island, St. Martin, which is a composite island having volcanic and limestone formations, has records of both surface and subterranean petroglyph sites.

Ceremonial Center

The research team from Island Resources Foundation (1980; Dick et al., 1980) deemed Fountain Cavern, because of its petroglyphs and midden deposit, a very important site worthy of further investigation. This task was undertaken in the 1980s by the newly formed Anguilla Archaeological and Historical Society (Douglas, 1986*b*). It was the AAHS that first determined the number of petroglyphs in Fountain Cavern and subsequently recorded and illustrated the 12 carvings (Douglas, 1986*a*). The AAHS also first interpreted Fountain Cavern as a ceremonial center used by prehistoric inhabitants of the island (Douglas, 1985). A ceremonial center attribution is in accord with the quantity and variety of subterranean petroglyphs, and other researchers have agreed with this interpretation. Petitjean Roget (1989) referred to Fountain Cavern as a ritual place, sacred place, magical cavern, and sanctuary, and Dubelaar (1989) referred to its use for religious or magical purposes. The dimly lit interior, poor ventilation, humid condition, and difficulty of access argue against Fountain Cavern having been a place of habitation. Also, some artifacts associated with habitation sites, such as chert flakes used in manioc preparation and shell celts, are absent at Fountain Cavern.

Some findings from the 1986 archaeological project support the hypothesis of some kind of ritual use of Fountain Cavern. First, all archaeological materials (apart from two sherds in test pit 2) were recovered in Chamber 1 (Fig. 6), the sector of the cavern containing the petroglyphs and the only part where daylight enters. All materials surface collected by the AAHS also came from Chamber 1. Thus, areas of Fountain Cavern that lacked petroglyphs generally also lacked artifacts. During the 1986 project, surface-collected prehistoric artifacts were found in Surface Areas A and B and the "washes" leading to test pit 1, all of which are in the general vicinity of Pool 1 (Fig. 6). The AAHS surface-collected materials were similarly concentrated.

Second, test pit 1 yielded by far the greatest density of ceramic remains, including 724 excavated sherds and 111 sherds from slumped walls (Tables 3 and 6). Test pit 1 is positioned between the base of the tall stalagmite (atop which is Petroglyph 12, Douglas' "Jocahu") and the truncated column with Petroglyph 11 ("Solar Chieftain"). The stalagmite (Fig. 7A, 28B) has the most impressive carving in Fountain Cavern; it is reasonable to suggest that this "statue" (Dubelaar, 1989) was central to ritual activity at Fountain Cavern as the Cueva Zemi stalagmite in Cuba was the focus of ritual offerings. The abundant sherds recovered in the test pit at the base of that stalagmite could be the remnants of ceramic vessels presented as ritual offerings to Petroglyph 12. Such vessels may have been placed in crevices below the petroglyph on the stalagmite. Sherds from the only two vessels exhibiting decoration (vessels 17 and 19) are from this test pit. Also, two conically-shaped radiolarian limestone tools, which may have been used to chip, grind, or otherwise create petroglyphs, were found in test pit 1, and the massive chopper came from nearby Surface Area A (Fig. 18).

Third, the artifact that is most suggestive of a ceremonial function, the three-pointer zemi (Fig. 19), came from test pit 1. Archaeological and ethnohistorical evidence has confirmed the ritual significance of such three-pointers among the Taino in the Greater Antilles. Also, the worn and blunt *Strombus* spine (Fig.

26A), a possible prototype three-pointer, and the *Oliva* shell that resembles in some ways a "tinkler" ornament (Fig. 26B) were recovered at the base of the stalagmite.

Support for the ceremonial center hypothesis for Fountain Cavern comes from the concentration of petroglyphs in the only area where daylight penetrates, their co-occurrence in Chamber 1 with the vast majority of the archaeological remains, the surface and excavated artifact densities near the stalagmite "statue" with Petroglyph 12, and the presence of a three-pointer and other artifacts that suggest ritual activity. A correlation also can be made with subterranean petroglyph sites in cavernous areas of the Greater Antilles, especially the Cueva Zemi site on Cuba, where remains of offerings were found. Fountain Cavern may have served as a regional ceremonial center used by Amerindians of Anguilla, as well as those of other islands, in view of the paucity of appropriate subterranean settings on the volcanic islands of the northern Lesser Antilles.

What has not been determined archaeologically are the kinds of rituals, ceremonies, religious practices, or zemiistic worship that took place in Fountain Cavern. Friar Pané's account of the cave on Hispaniola with two stone zemis, which the Taino supplicated for rain in times of drought, suggests one ritual that might have occurred in Fountain Cavern since Anguilla also suffers periodic drought.

Although some findings from the 1986 research can be invoked in support of the ceremonial use hypothesis for Fountain Cavern, that does not preclude the possibility that other activities took place as well, and some artifacts may relate to those activities. For ceramic vessels, two alternative hypotheses are reasonable. First, some sherds may be the remains of ceramic burial urns, a funerary practice reported, although not commonly, from elsewhere in the Antilles. Lovén's (1979: 130) admonition about not too strongly differentiating between burial and shrine caves could pertain here because urn burial can be viewed as another ritual manifestation. The four Mammalia sp. long bones from the cavern floor and test pit 1 might be remnants of disturbed burials, although it is not certain that the bones are human.

Another plausible argument for the presence of some ceramic sherds is that they are the remains of containers used for the collection and transport of water. The existence of permanent freshwater sources in Fountain Cavern was known by the historic occupants of this periodically drought-stricken island. Assuming these pools existed prehistorically, it is reasonable to presume that the Amerindian inhabitants of Anguilla also would have been aware of the freshwater sources. The abundant sherds in test pit 1, located beside Pool 1, could be interpreted as the remnants of ceramic vessels broken during water collecting activities, as it has been suggested that some pieces of plastic found in test pit 1 are the remains of modern water containers. The absence of prehistoric sherds at Pool 2 might contradict a water collecting hypothesis and, therefore, supports a purely ritual function for test pit 1 ceramics, but such an argument really is untenable. Pool 2 is located in the deeper and darker recesses of Fountain Cavern while Pool 1, located closer to the entrance, is a much more easily accessible water source. Also, a lack of prehistoric ceramics at Pool 2 is matched by the absence of modern plastic pieces, which suggests that Pool 2 never has been a favored water collection point.

The ceremonial, urn burial, and water procurement hypotheses all have merit, but the data from surface and excavated sherd distributions and the ritual artifacts more strongly support the conclusion that Fountain Cavern was a ceremonial center for the Amerindians of Anguilla.

Cultural Affiliation

A total of 2493 objects, including artifacts, miscellaneous materials, and faunal remains, were recovered in Fountain Cavern during the 1986 project. Table 12 summarizes these objects by excavation units (test pits 1–3) and surface/disturbed areas. Excavated units yielded far more objects (N = 2037; 81.7%) than surface/disturbed areas (N = 456; 18.3%). All objects in each test pit are regarded as being from a single unit. Test pit 1 has 1398 objects (68.6%), test pit 2 has 15 (0.7%), and test pit 3 has 624 (30.6%) of the 2037 excavated objects.

Three categories stand out, both for excavated and total objects. Prehistoric ceramic sherds (N = 775 excavated, 944 total) are followed in quantity (and percentage) by invertebrates (N = 586 excavated, 702 total) and speleothems (N = 463 excavated, 598 total). Table 12 also shows that prehistoric ceramics constitute extremely high percentages of the excavated prehistoric artifacts (775 of 779; 99.5%) and total prehistoric artifacts (944 of 950; 99.4%). Indeed, the inventory of non-ceramic prehistoric artifacts at Fountain Cavern is exceedingly restricted when compared to the quantity and diversity of such artifacts in open habitation sites.

Prehistoric ceramics provide the data most pertinent to the issue of cultural affiliation. Earlier in this paper, the bulk of excavated ceramics was attributed to the post-Saladoid period, based on detailed ceramic analysis (Petersen and Watters, 1991). Of 780 sherds and fragments available for study, 234 (30%) were assignable to specific vessels. Of the 234 specimens, 229 (97.9%) displayed no decoration. Sherds and fragments not assigned (N = 546) to particular vessels exhibited no decoration (although in some cases their surfaces were too worn to determine whether decoration originally was present). Thus as many as 775 of 780 excavated specimens (99.4%) may have been undecorated. At the vessel level, 27 of 29 (93.1%) vessels defined from excavated sherds had no decoration. For sherds collected by the AAHS (but excluding the 650 fragments), 5934 of 5954 (99.66%) sherds lacked decoration. Thus, undecorated ceramics predominate in all major analytical categories.

The abundance of undecorated sherds in the Fountain Cavern sample is one line of evidence supporting the post-Saladoid attribution. However, other attributes, such as folded or thickened rims, a preponderance of incurvate vessel forms, and minor usage of white-on-red (WOR) painting and broad-lined incision, further support a post-Saladoid cultural affiliation for the Fountain Cavern ceramics (Petersen and Watters, 1991).

Five of 780 (0.6%) sherds in the Fountain Cavern excavated ceramic sample available for study are decorated; they constitute five of 234 (2.1%) specimens assigned to vessels. One relatively thick sherd, the sole vessel 19 sherd, displays a single, deep, U-shaped incision (Fig. 17J). Such broad-line incision is most often attributed to the post-Saladoid period. Eight (0.1%) of the 5954 assignable sherds that were surface collected by the AAHS are painted (7 WOR and one painted handle) and 12 (0.2%) have modelled decoration.

Four excavated sherds exhibit white-on-red (WOR) geometric painting (Fig. 17I), a decorative feature that is generally regarded as characteristic of earlier Cedrosan Saladoid pottery. Indeed, both white-on-red painting and zoned-incised-crosshatch decoration (the latter absent at Fountain Cavern) are regarded as di-

Table 12.—*Summary table of the artifacts, miscellaneous materials and faunal remains from excavated and surface/disturbed contexts at Fountain Cavern, Anguilla.*

Category	Test pit 1 (D1-3 to -17)	Test pit 2 (D1-19)	Test pit 3 (D1-20 to -24)	Total	Surface Area A (D1-1)	Surface Area B (D1-2)	Test pit 1 (slump) (D1-18)	Pool 1 (D1-25)	Petroglyph (D1-26)	Total	Grand total by category
Prehistoric											
Ceramic	724	2	49	775	37	20	111	1	—	169	944
Lithic	2	—	1	3	2	—	—	—	—	2	5
Three-pointer	1	—	—	1	—	—	—	—	—	0	1
Total	727	2	50	779	39	20	111	1	0	171	950
Historic/modern											
Ceramic	—	—	6	6	—	—	—	—	—	0	6
Glass	6	—	31	37	3	2	3	—	—	8	45
Plastic	35	—	1	36	1	—	8	—	—	9	45
Metal	2	—	8	10	3	—	1	—	—	4	14
Total	43	0	46	89	7	2	12	0	0	21	110
Miscellaneous											
Speleothem	373	12	78	463	31	1	101	—	2	135	598
Other material											
Unusual rock	8	—	1	9	3	—	—	—	—	3	12
Botanical	—	—	1	1	—	—	—	—	—	0	1
"Fossil wood"	—	—	1	1	—	—	—	—	—	0	1
Organic	—	—	104	104	—	—	—	—	—	0	104
Crust	—	—	—	0	—	—	—	2	—	2	2
Wood	—	—	—	0	3	—	—	—	—	3	3
Total	381	12	185	578	37	1	101	2	2	143	721
Invertebrates	244	—	342[a]	586	7	—	109	—	—	116	702
Vertebrates	3	1	1	5	3	—	2	—	—	5	10
Total	247	1	343	591	10	0	111	0	0	121	712
Grand total by area	1398	15	624	2037	93	23	335	3	2	456	2493

[a] = Includes 230 land snails.

agnostic of early Caribbean ceramics, dating perhaps as far back as 200–300 B.C. (Rouse, 1989). Some archaeologists have argued the WOR sherds represent an older decorative style that is incongruous with the postulated post-Saladoid use of Fountain Cavern. This led to some speculation concerning use of Fountain Cavern by Saladoid peoples, prior to its use by post-Saladoid populations.

However, one does not have to invoke a Saladoid presence in Fountain Cavern to account for surface and excavated WOR sherds. If the sherds really are earlier Saladoid sherds, they may have been introduced much later into the deposits by post-Saladoid peoples who picked them up elsewhere. In fact, in view of the scarcity of decorated sherds, an argument for incidental inclusion of WOR sherds in the deposits seems more logical. If the sherds are not early Saladoid, they may represent persistence of white-on-red decoration into later Saladoid ceramic styles, as with the Mill Reef style on Antigua, and perhaps into certain post-Saladoid ceramics on a very limited basis. White-on-red painting is not a major decorative feature in either instance.

The term "post-Saladoid" is used throughout this paper in juxtaposition to the term Saladoid, thereby indicating a temporal difference. The Saladoid series (Rouse and Allaire, 1978), more recently the Cedrosan Saladoid subseries (Rouse, 1986: 139), is based on specific ceramic styles, modes, or attributes present during a particular timespan in the West Indies. Ceramics that postdate the Saladoid series in the northern Lesser Antilles are placed in the Elenan Ostionoid ceramic subseries by Rouse (1986:143–144). Elenan Ostionoid styles differ from Cedrosan Saladoid styles and they occur later in time.

In this paper, the term post-Saladoid indicates ceramic forms that differ from and are more recent than Saladoid pottery. However, because the ceramics from Anguilla are not yet assigned to specific styles or subseries, one cannot equate the term post-Saladoid with Rouse's Elenan Ostionoid subseries. Among northern Lesser Antilles archaeologists, Goodwin (1979:305) and Watters (1980:274) have been particularly reluctant to apply the Elenan Ostionoid (formerly Elenoid) designation to post-Saladoid ceramics since their specific attributes are not well defined. One reason they are poorly defined is that the ceramics overwhelmingly are undecorated, so one cannot use decorative motifs (which was one attribute used to define the Cedrosan Saladoid subseries) to define the post-Saladoid ceramics. Definition of specific post-Saladoid ceramic styles will have to rely on other attributes, notably vessel morphology including shape and rim form (Petersen and Watters, 1991) and possibly distinctive temper associations (Donahue et al., 1990).

The distinction between Saladoid and post-Saladoid in the northern Lesser Antilles has other implications. Foremost among these is the issue of when Saladoid ends and when post-Saladoid begins on any given island. By roughly A.D. 600–700, ceramic styles that are attributed to the Cedrosan Saladoid subseries *begin* to disappear from the archaeological record in the northern Lesser Antilles. Yet, certain elements persist for a longer time period on some islands, such as Antigua's Mill Reef style, which was the last Saladoid manifestation on that island. A clearly defined temporal boundary between Saladoid and post-Saladoid has yet to be established for most islands in the northern Lesser Antilles, and the temporal boundary may differ for each island.

Anguilla, because of its location in the northern Lesser Antilles and its proximity to the eastern Greater Antilles, potentially will play an important role in establishing Saladoid and post-Saladoid ceramic styles, temporal boundaries, and spatial distributions on both sides of the Anegada Passage. Unpublished research at two open sites on Anguilla, Rendezvous Bay (AL2) and Sandy Ground (AL3), suggests similarities between post-Saladoid manifestations in these areas.

CONCLUSIONS

Fountain Cavern served as a ceremonial center for the post-Saladoid populations of Anguilla after about A.D. 600, and more specifically A.D. 900–1200, or later. Although the possibility of earlier Saladoid use should not be dismissed, the weight of evidence supports post-Saladoid use of Fountain Cavern. The 12 well-preserved petroglyphs assuredly related to some form of ritual activity. The archaeological materials indicate this was not a habitation site. Post-Saladoid ceramics, the bulk of which are undecorated, most likely were involved in rituals (possibly including urn burial) and also may have been used to procure fresh water. Shattered speleothems indicate that Fountain Cavern has been severely jolted in the past, probably by earthquakes. Active and passive taphonomic processes resulted in the admixture of archaeological deposits from different time periods. Historic and modern artifacts show that Fountain Cavern continued to be used for collecting water, if no longer for rituals, by later inhabitants of this periodically drought-stricken island. The petroglyphs of Fountain Cavern, a rare type site in the northern Lesser Antilles, demand adequate protection.

FUTURE DEVELOPMENT OF FOUNTAIN CAVERN

Fountain Cavern is a very important archaeological resource among the islands of the northern Lesser Antilles because its petroglyphs have suffered little damage from vandalism and are extremely well preserved. Their preservation is due, in large part, to three factors: (1) their discovery occurred only relatively recently and was kept secret (Douglas, 1986*b*); (2) they have been afforded some degree of protection by their inclusion in the Fountain National Park established by the Government of Anguilla; and (3) the Anguilla Archaeological and Historical Society installed a lockable metal grid across the entrance. While the first factor may be considered fortuitous, the other factors indicate genuine concern for protecting these archaeological resources. Concern for the island's archaeological and historical heritage on the part of Anguillians, Government, and the AAHS led to enactment of the "Antiquities Ordinance, 1982" to protect such resources. The findings at Fountain Cavern were instrumental in fostering that ordinance.

Scientists involved in the Fountain Cavern study (see reports in Gurnee, 1989) have cautioned that any plan of development must be devoted to preserving and enhancing the natural and cultural environments in the cavern. Fountain Cavern has the potential to serve two roles simultaneously. An above-ground museum/interpretation center could serve an educational role for informing Anguillians about natural history and Amerindian prehistory of their island. An economic role for Anguilla would be served by promoting visits to the site by tourists. But any development scheme for the site must take into account the high probability areas (Fig. 29) for concentrations of archaeological materials.

ACKNOWLEDGMENTS

The Fountain Cavern archaeological study was supported by grants from the Canadian International Development Agency (to the Government of Anguilla), the M. Graham Netting Research Fund of Carnegie Museum of Natural History, the Charles Cohn Foundation, and Eugene M. Grant. David Carty, President, and Nik Douglas, Secretary, of the Anguilla Archaeological and Historical Society extended the invitation to conduct the research and arranged with Government to secure the permits. For assistance in excavating the test pits, I am indebted to David Carty, Tim Hodge, Nik Douglas, Don Mitchell, Penny Slinger, Bridgette McCarthy, Roland Richardson, and especially Andy Graff, a student from DePauw University who devoted much time and effort to the project while on school vacation. People at various institutions aided the research: Edward J. Petuch (Florida Atlantic University), fossil mollusk identification; Richard A. Howard (then of Arnold Arboretum, Harvard University), comments on the *Clusia* tree; Elizabeth J. Reitz and James W. Porter (University of Georgia), vertebrates and corals respectively; Ross MacPhee (American Museum of Natural History) and Donald A. McFarlane (Natural History Museum of Los Angeles County), *Amblyrhiza inundata*; James B. Petersen (University of Maine at Farmington), ceramic study; Gina Douglas (Linnean Society of London), Anguilla map; Jay Haviser (Archaeological–Anthropological Institute of the Netherlands Antilles), access to lithic specimens; and Irving Rouse (Yale University) and Samuel M. Wilson (University of Texas at Austin), pertinent references. At the Anguilla Archaeological and Historical Society, David Carty provided requested geographic information and Nik Douglas verified counts of materials left on Anguilla and provided information about AAHS surface collections from Fountain Cavern. Assistance provided by staff and research associates of Carnegie Museum of Natural History included Juan J. Parodiz, Curator Emeritus, Section of Malacology, land snails and the *Serpulorbis* and *Lucina* specimens; Research Associates Frances B. King, botanical identification, and Robert Stuckenrath, chemicals used in her study; Richard A. Souza, Collection Manager, Section of Minerals, speleothems, permineralized wood, calcite, and organics; Fred Utech, Curator of Botany, permineralized wood growth rings; Nancy J. Perkins, Gail Richards, and Melinda Carmichael, Exhibit Design and Production, assistance with figures; and from the Section of Anthropology, Stanley W. Lantz, photographs, Sylvia M. Keller, manuscript preparation, especially tables, and volunteers Tara M. Reilly and Michelle A. Blaskovich with lab work. I am indebted to Chief Minister Emile R. Gumbs, members of the Fountain National Park Development Committee, the National Speleological Foundation, and many Anguillians whose interest in the 1986 archaeological project has been gratifying. This paper benefited greatly from the careful reading and helpful comments of the editors and reviewers. Watters and Petersen presented portions of this article in preliminary form at the 1989 Society for American Archaeology meeting in Atlanta.

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ANNALS OF CARNEGIE MUSEUM
VOL. 60, NUMBER 4, PP. 321–357 27 NOVEMBER 1991

AMERINDIAN CERAMIC REMAINS FROM FOUNTAIN CAVERN, ANGUILLA, WEST INDIES

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ABSTRACT

Fountain Cavern on the island of Anguilla in the West Indies is a subterranean archaeological site containing prehistoric petroglyphs, artifacts, and faunal remains and, as such, is a rare occurrence in the northern Lesser Antilles. Amerindian ceramics were the predominant artifact category recovered from Fountain Cavern in 1986 during test excavations and limited surface collection. Of 780 specimens, 29 fragmentary ceramic vessels are defined with vessel lot and attribute-based methods, and 234 specimens are assigned to specific vessels. The Fountain Cavern ceramics are distinctive although generally similar to other post-Saladoid ceramics in the West Indies. The likelihood of interisland social interaction is inferred from ceramic temper data. The Fountain Cavern ceramics may be generally related to the Elenan Ostionoid subseries and apparently represent the remains of Amerindian ritual activities after ca. A.D. 600, and more specifically ca. A.D. 900–1200 or later.

INTRODUCTION

Amerindian ceramics are the predominant category of cultural remains recovered during archaeological testing in 1986 at Fountain Cavern, Anguilla, in the northern Lesser Antilles, West Indies. Fountain Cavern is unusual among Lesser Antilles archaeological sites in its subterranean setting and cultural remains. Various petroglyphs, Amerindian ceramics, associated fauna, and other remains are attributable to late prehistoric usage of Fountain Cavern, almost certainly for activities other than habitation. All of the ceramics, possibly excepting one vessel, document post-Saladoid usage of Fountain Cavern after ca. A.D. 600, and possibly more specifically A.D. 900–1200 or later. This report documents a substantial sample of the Amerindian ceramics from Fountain Cavern and complements a more complete report on the 1986 testing (Watters, 1991).

PHYSICAL SETTING

Anguilla occupies a pivotal location in the northeast portion of the Caribbean Sea. It is the most northerly of the relatively large islands in the Lesser Antilles chain, which stretches from Grenada in the south (lat. 12°N) to Sombrero in the north (lat. 18.5°N), and it lies 125 km east of the Virgin Islands, the easternmost group in the Greater Antilles. The closest major island is St. Martin located about 10 km south of Anguilla (Fig. 1).

Anguilla (including Scrub Island) is approximately 30 km (18.6 mi) long, with a maximum width of about 5.9 km (3.7 mi) and an area of about 91 km^2 (35 mi^2) (Fig. 2). Its surficial geology consists almost exclusively of limestone over largely

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Submitted 20 August 1990.

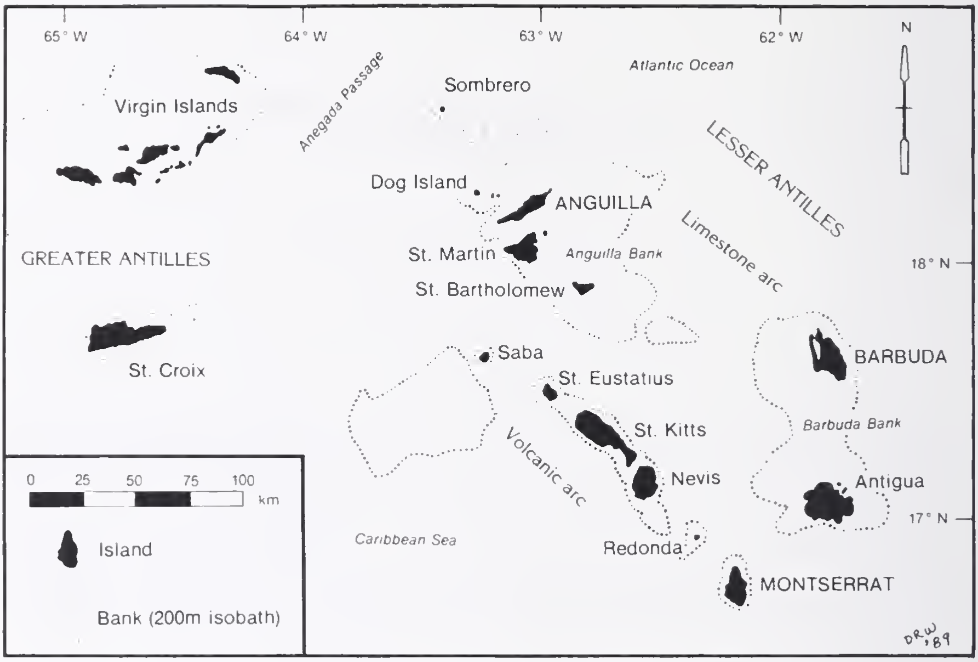

Fig. 1.—Islands and banks of the northeastern Caribbean Sea (eastern Greater Antilles and northern Lesser Antilles).

obscured volcanic rocks. However, a few restricted exposures of altered andesitic tuff and altered basalt occur on the surface of the island. Although the exact maximum elevation is unclear, a discontinuous ridge near the north coast exceeds 61 m (200 ft) above sea level. Soils are relatively thin across Anguilla, consisting of a reddish-brown stony clay *terra rosa* in the uplands and a gray or black, poorly drained rendzina in the low areas. Limestone bedrock protrudes all across the island, but is especially prominent on the east and west headlands. Rainfall is limited and seasonal; relatively few natural sources of fresh water are present on the surface of Anguilla. The natural vegetation has been significantly altered, but likely consisted of evergreen bushland prior to modern disturbances, along with more limited areas of grassland, manchineel, mangrove, strand and rock pavement vegetation (see Watters, 1991, for expanded treatment of Anguilla's physical setting and natural history).

Anguilla is a narrow, dry, and relatively flat island that epitomizes the "Limestone Caribbees" forming the outer arc of the northern Lesser Antilles. These carbonate islands stand in stark contrast to the rugged, mountainous islands of the volcanic, inner arc of the Lesser Antilles. Volcanic and limestone rocks occur together on a few "composite" islands, such as St. Martin and Antigua. Differences in the prehistoric archaeological record of the volcanic and limestone islands also are evident in terms of available food resources (e.g., Watters and Rouse, 1989) and apparently the onset of occupation (e.g., Watters, 1980:334–336). Limestone and volcanic islands also can be expected to produce different suites of "grit" (rock) and sand temper, as typically employed by Amerindian potters in the Lesser Antilles, and these differences potentially enable the tracing of the movement of

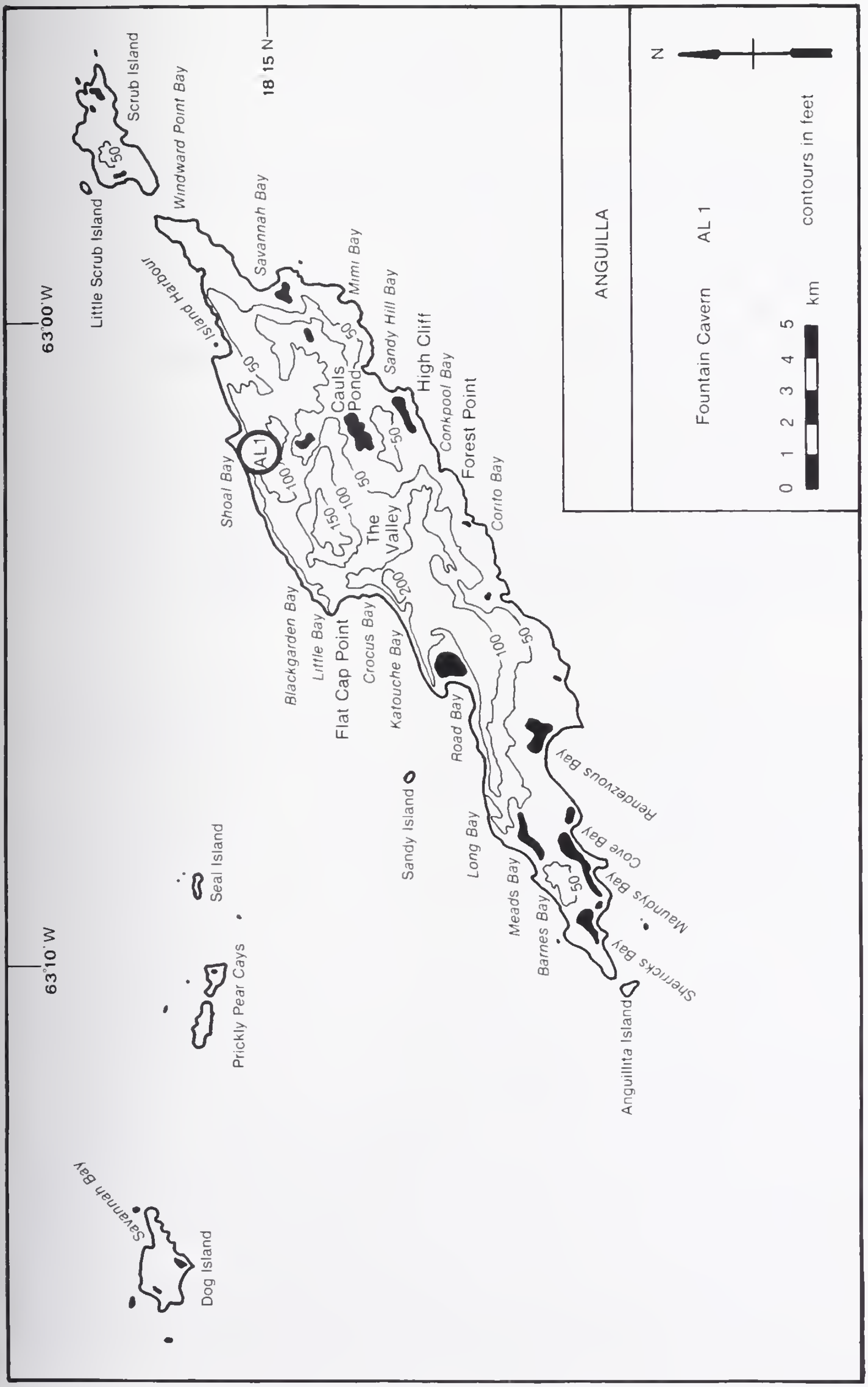

Fig. 2.—Topography of Anguilla and location of Fountain Cavern (AL1) prehistoric site.

ceramic vessels and/or temper materials between islands (e.g., Donahue et al., 1990).

FOUNTAIN CAVERN ARCHAEOLOGY

Background

Fountain Cavern is located in the first national park established by the Government of Anguilla. The park is situated on the north coast of the island at Shoal Bay. Fountain Cavern lies in the southern sector of the park about 250 m inland from the coast.

Between 6 and 16 January 1986, research at Fountain Cavern was undertaken at the request of the Anguilla Archaeological and Historical Society (AAHS) and the Government of Anguilla to assess the archaeological resources within the cavern. The study was necessary because Fountain Cavern is being considered for development as a facility to enhance Anguilla's tourism.

Prehistoric remains were known from Fountain Cavern prior to the 1986 research. Although the presence of petroglyphs had been previously noted, the site was first recorded formally in 1979 by a research team from the Island Resources Foundation who verified the petroglyphs, reported evidence of other remains including ceramics, and identified 19 archaeological sites on Anguilla. Subsequently, in the 1980s, the newly formed AAHS surface-collected artifacts and recorded 12 petroglyphs at the site (Douglas, 1985, 1986*a,* 1989). AL1 is the site designation for Fountain Cavern.

Field Methods

Field methods involved a general survey of the floor of the cavern, excavation of test pits in selected parts of the cavern, and examination of known petroglyphs. At the request of the AAHS, the majority of the time spent in Fountain Cavern was devoted to excavation of test pits (Watters, 1991).

From an archaeological standpoint the cavern can be divided into two chambers (Fig. 3; see also Gurnee, 1989: plans 3, 4). Chamber 1 includes the area beneath the entrance and the domed ceiling in the front of the cavern and contains almost all of the observed cultural remains. Chamber 2 begins at a raised platform occupying the middle part of the cavern and continues west into its deepest recesses.

Fountain Cavern is entered vertically by way of a steel ladder. Under the entrance is a relatively level area from which the floor of Chamber 1 slopes sharply downward to the southeast, south, and southwest. Pool 1, a freshwater pool, is found along the south wall of Chamber 1. The floor of Chamber 2 is flatter than the steeply sloping floor of Chamber 1.

Extensive spalling from the ceiling and walls has occurred in Fountain Cavern and sediment depths are quite different between the chambers. In Chamber 1, major sediment deposits occur beneath the entrance, on the slope, and against the southeast and south walls. These deposits are composed of large quantities of coarse rock spall and only limited finer sediment. Sediment deposition in Chamber 2 has been negligible.

Three test pits were excavated in Fountain Cavern, two in Chamber 1 and one on the raised platform in Chamber 2. Each test pit was 1 m^2 and dug to bedrock. All natural and cultural materials were removed from each test pit. Deposits were screened through ⅛-inch mesh hardware cloth and cultural remains were segregated and bagged by units.

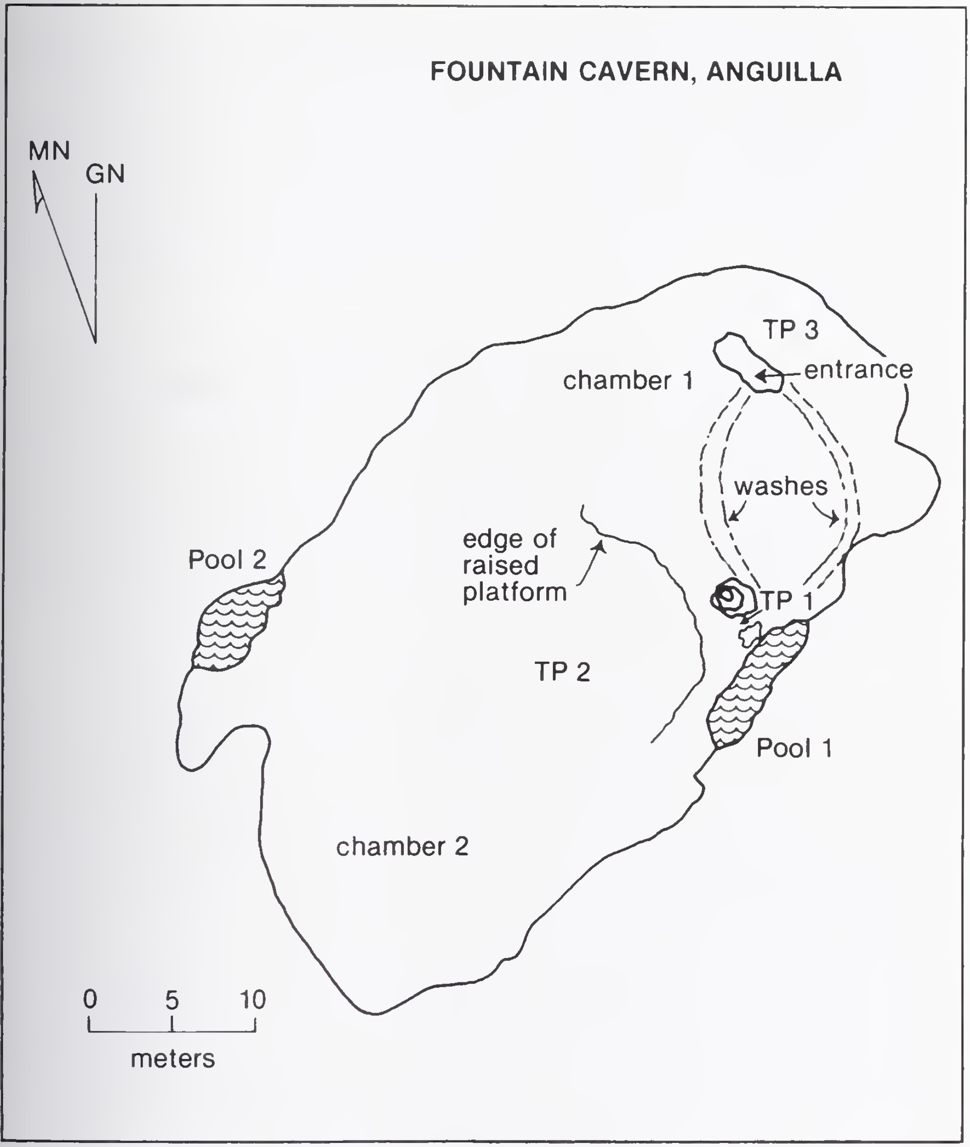

Fig. 3.—Generalized planview of Fountain Cavern showing the positions of chambers and test pits.

Test pit 1 in the southwest section of Chamber 1 was between the base of the large stalagmite with Petroglyph 12 and the base of a nearby flat-topped stalagmite with Petroglyph 11. Four strata were identified in test pit 1, but Stratum 4 was the principal deposit, extending to about 155 cm below the surface. The matrix included fragmented rocks and broken speleothems around which were cavities containing patchy accumulations of finer sediment. Excavation of test pit 1 was complicated by intrusion of the stalagmite base into the pit. The stalagmite occupied almost 50% of the bottom area of test pit 1 (see Watters, 1991: fig. 11).

Artifacts were found throughout test pit 1, some of which had slid downward through the crevices and holes among the rocks in Stratum 4. Modern coins, bits of plastic, and pieces of glass were found in several lower levels of test pit 1. As discussed below, cultural remains clearly were mixed at different depths and cannot be regarded as having been recovered from reliable stratigraphic contexts.

The second test pit, in Chamber 2 on the raised platform in the middle of the cavern, was excavated to confirm the apparently shallow depth of deposit and the paucity of artifacts in that area. The sediment in test pit 2, composed of bat excrement and decomposing limestone, did not exceed 5 cm above bedrock across most of the test pit. Two pieces of partially buried prehistoric pottery were recovered from the surface.

Test pit 3 was dug on the east side of the relatively level area beneath the entrance to Fountain Cavern. This location was chosen because of its position at the only known entrance to the cavern, its proximity to a number of petroglyphs, and the expected depth of sediment there. Two strata were identified in test pit 3. Stratum 1 overlies bedrock to a depth of about 30 cm. A number of crevices and holes penetrate into the bedrock and a fissure near the northwest corner reaches a depth of about 75 cm. Stratum 2 sediment occurred in these crevices and holes. Artifacts were recovered only from Stratum 1, which yielded both prehistoric and historic objects throughout the test pit. As in test pit 1, the artifacts occurred in a somewhat mixed context.

Radiocarbon Dating

Two shell (*Cittarium pica*) samples from test pit 1 were submitted to Beta Analytic, Inc., of Coral Gables, Florida, for radiocarbon dating. The first shell sample (AL1-RC1) yielded a date of 1220 ± 70 B.P. (Beta-15485), the second (AL1-RC2) 1130 ± 80 B.P. (Beta-15486). Conversion to the Christian calendar using the radiocarbon standard of A.D. 1950 indicates a date of A.D. 730 (range with one standard deviation of A.D. 660–800) for the first sample and a date of A.D. 820 (range of A.D. 740–900) for the second sample. The first shell was found at a depth of about 60 cm and the second at 72 cm. A small charcoal sample (AL1-RC3) from a depth of about 100 cm in test pit 1 dated to 1530 ± 140 B.P. (Beta-15824), or A.D. 420 (range of A.D. 280–560). None of these dates have been corrected given various questions about their reliability (see Watters, 1991).

Thermoluminescence dating on two sherds (Alpha-2872, -2873) from test pit 1 was unsuccessful because of "anomalous fading," which most likely resulted from the presence of volcanic minerals in the sherds (report from Alpha Analytic, Inc., of Coral Gables, Florida).

Recovered Artifacts

A total of 2493 artifacts, faunal remains, and miscellaneous materials were recovered from Fountain Cavern during the 1986 fieldwork (Watters, 1991). Of these, 2037 (81.7%) originated in test pits 1, 2, and 3; 121 (4.9%) were collected from the cavern floor; and 335 (13.4%) came from uncertain provenience due to the collapse of some sediments in test pit 1. These materials have been classified as prehistoric ceramics, lithics, and a three-pointed stone; historic and modern ceramics, glass, plastic, and metal; miscellaneous materials including speleothems (cave deposits), unusual rock, botanics, "fossil wood," organics, calcium carbonate crusts, and wood; and taxa of invertebrate and vertebrate faunas (Watters, 1991: tables 3–12).

Amerindian ceramic sheds dominated the artifact inventory, comprising 944 specimens. Of these, 782 (those with established provenience from excavated contexts and a few surface-collected specimens) were returned to the United States for analysis. Two were sacrificed for thermoluminescence dating and the other 780 specimens are reported here. Excluded from this study are sherds from disturbed contexts and most of the surface sherds collected by Watters in 1986, all of which were left on Anguilla, and an estimated 5000 to 5500 surface sherds (Douglas, 1985:11, 1986*a*:28) collected by various members of the AAHS prior to Watters' testing at Fountain Cavern.

ANALYTICAL METHODS

Collaborative analysis of Amerindian ceramics from Fountain Cavern was undertaken in the Section of Anthropology, Carnegie Museum of Natural History, with subsequent examination of these remains at the University of Maine at Farmington. A standard vessel lot analysis was conducted. Vessel lot analysis is a technique previously applied to samples of Amerindian hand-built ceramics from northeastern North America (e.g., Petersen, 1980, 1985; Petersen and Power, 1985). The technique was first applied in the Caribbean region to Afro-Montserratian ceramics from the Harney site slave cemetery (Petersen and Watters, 1988) and is here applied to Caribbean Amerindian ceramics from the first time.

Vessel lot analysis attempts to reconstruct vessels, define the minimum number of individual vessels in a sample, and provide detailed documentary and comparable ceramic data. Such analysis can help correlate natural and archaeological strata, cultural features, and other provenience units of an archaeological site; assignment of ceramic specimens, like actually conjoining sherds, to a particular vessel establishes their common origin and contemporaneity.

Twenty-nine ceramic vessels were defined from a sample of 228 sherds and three fragments (30%) out of an available sample of 704 sherds and 76 fragments from Fountain Cavern (Fig. 4–7). Ceramic sherds minimally preserve both interior and exterior surfaces, whereas fragments preserve one or another or no original surfaces.

The defined vessel lots are described below by various attribute categories, or modes (Rouse, 1939:11–72, 1960, 1977). These ceramic modes (e.g., temper, texture, manufacture, etc.) represent potentially diagnostic attributes that *may* be discrete in temporal and/or spatial dimensions and therefore are of particular importance in archaeological research (see Tables 1 and 2).

Microscopic analysis of West Indian sherds has been rarely undertaken. This analysis combines microscopic and macroscopic techniques. Petersen first conducted a macroscopic analysis of the entire available ceramic sample trying to match specimens without consideration of associated provenience data. Sherds and fragments not assignable to a specific vessel were excluded from further analysis. Each tentatively defined vessel lot was then subjected to a detailed attribute analysis for each ceramic mode. Each specimen assigned to a specific vessel was carefully re-examined macroscopically and microscopically using a variable power binocular microscope (10×–50×). Geologist Gary Laverdiere at the University of Maine at Farmington later corroborated and refined Petersen's initial temper identifications. Measurements were taken with needle-nose calipers accurate to 0.05 mm. Color values were recorded using Munsell soil color charts (Table 2).

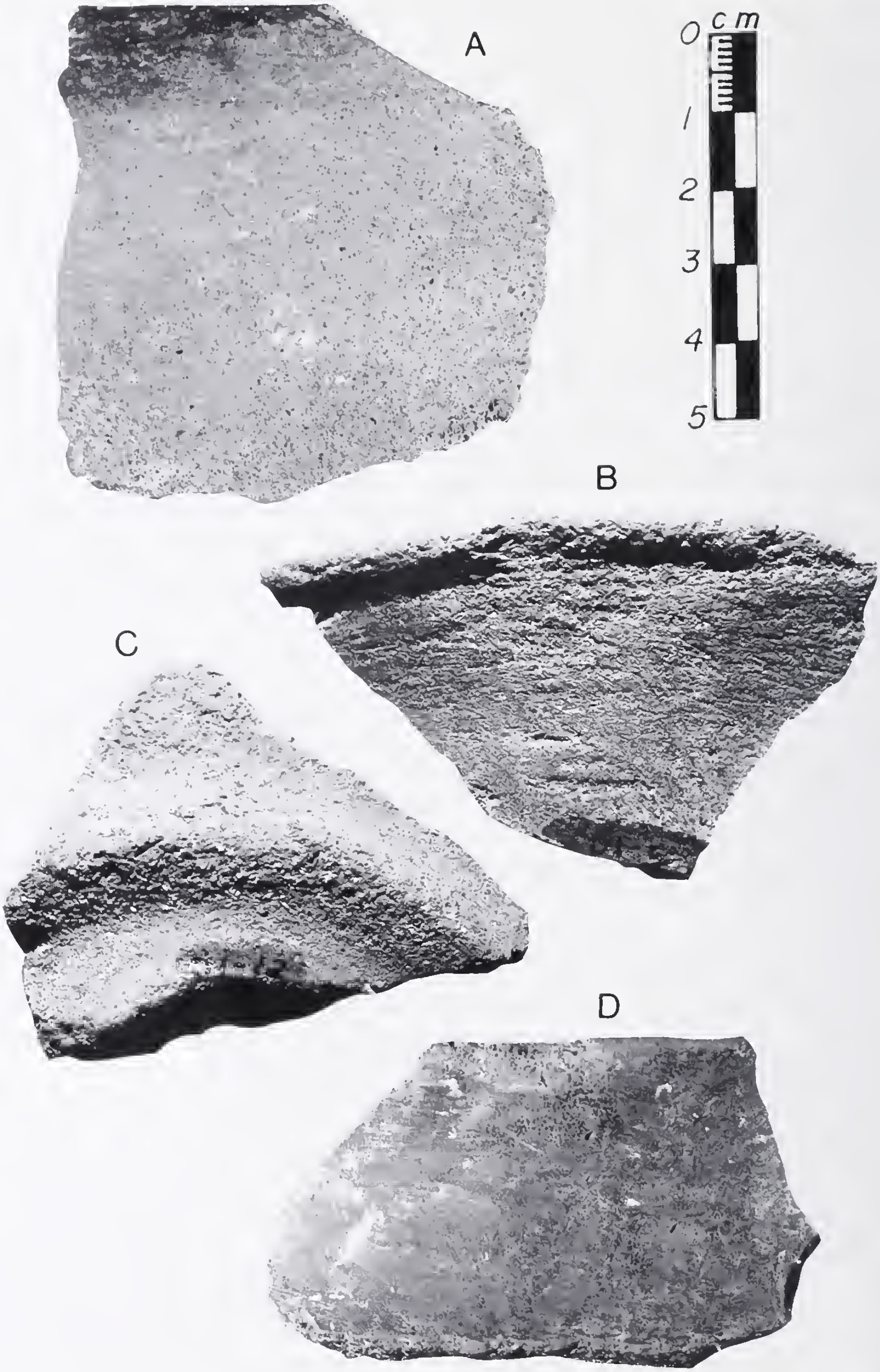

Fig. 4.—Amerindian ceramics from Fountain Cavern. A. Exterior surface of vessel 2 rim sherd showing burnished finish. B. Exterior surface of vessel 3 rim sherd showing smoothed, somewhat irregular finish, and additive coil forming lip. C. Exterior surface of vessel 5 basal sherd showing smoothed finish, and pedestaled construction. D. Exterior surface of vessel 8 rim sherd showing burnished finish, and coil fracture on lower edge.

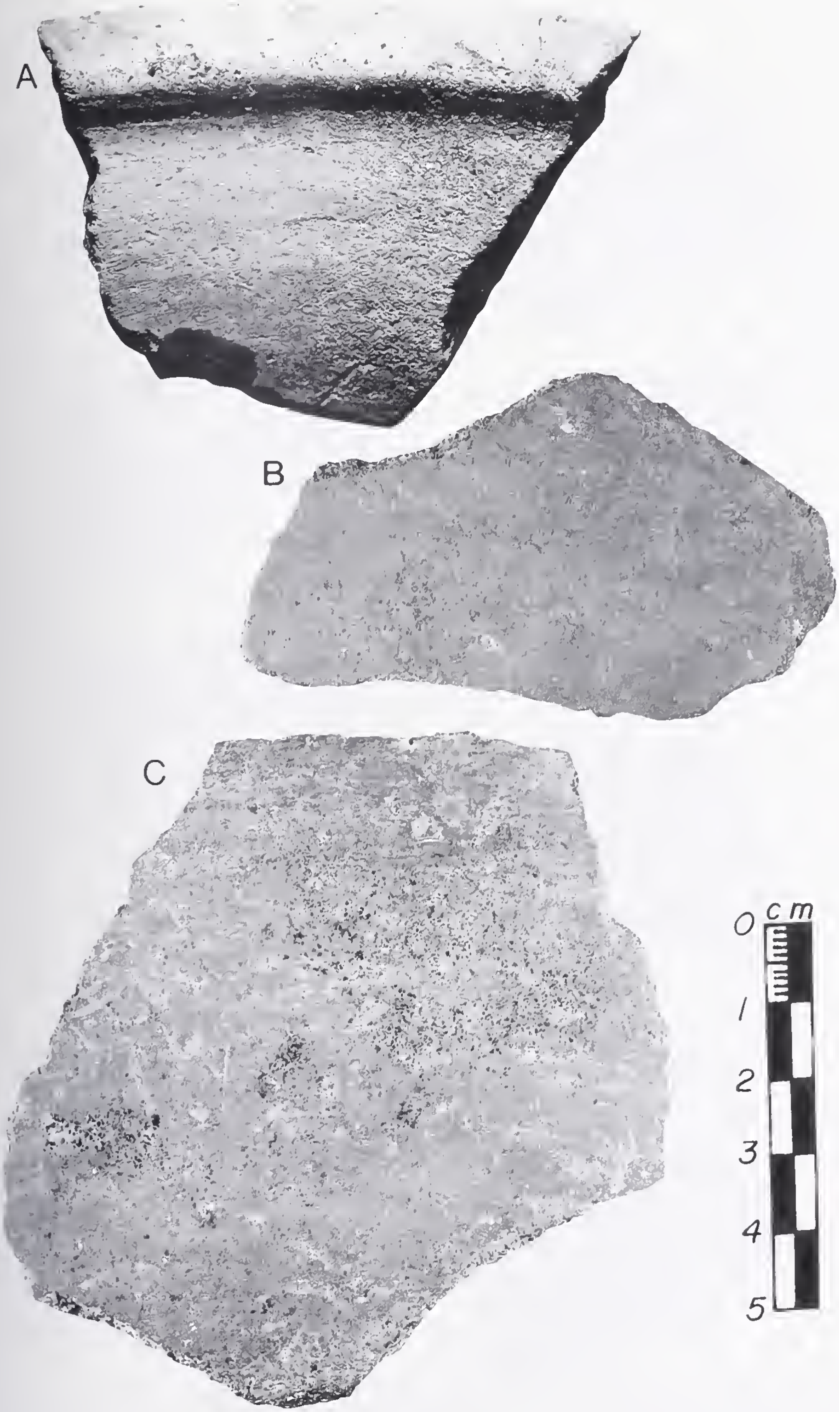

Fig. 5.—Amerindian ceramics from Fountain Cavern. A. Interior surface of vessel 24 rim sherd showing slipped and burnished finish on additive coil forming lip, and burnished interior finish. B. Exterior surface of vessel 24 body sherd showing burnished finish. C. Exterior surface of vessel 29 body sherd showing burnished finish.

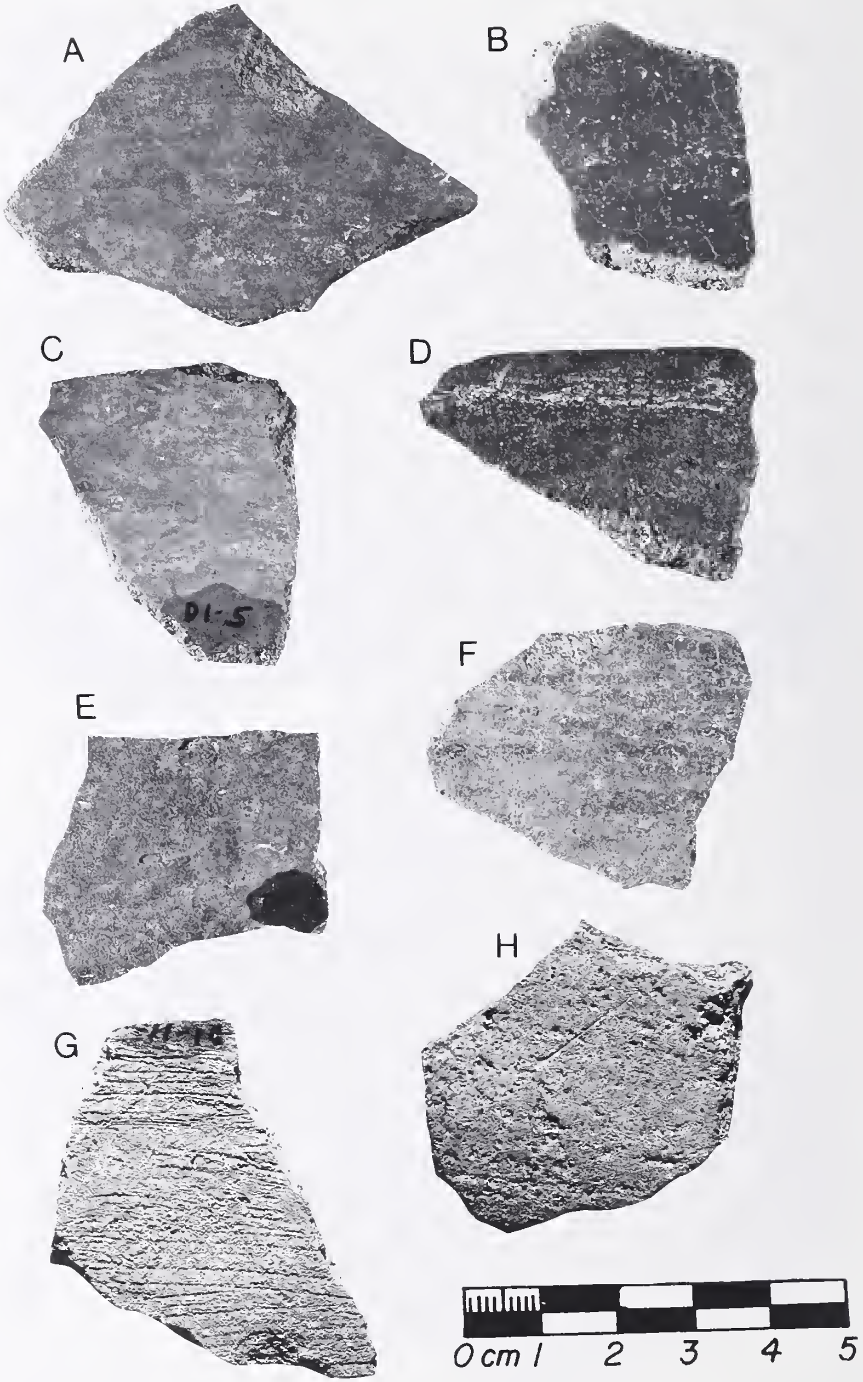

Fig. 6.—Amerindian ceramics from Fountain Cavern. A. Exterior surface of vessel 3 body sherd showing smoothed finish. B. Exterior surface of vessel 4 body sherd showing slipped and burnished finish. C. Interior surface of vessel 4 body sherd showing burnished finish. D. Exterior surface of vessel

CERAMIC VESSELS

Temper

The temper in the defined vessels is similar and typically includes several distinctive temper constituents (Table 1; Fig. 8). Sharp angular quartz predominated in nearly all of the vessel pastes. The total temper comprises about 30–40% of the paste in 16 vessels (55%), over 40% in ten vessels (35%) and less than 30% in three vessels (10%). These frequencies include the presence of various other angular minerals with the quartz in at least 19 vessels, including feldspar, pyroxene, amphibole, tourmaline, schist, and garnet, among others, collectively subsumed within an "other" category. However, these other minerals are less well represented than the quartz in nearly every case. The quartz and other minerals are predominantly fine-grained in all vessels, less than 1.0 mm in maximum dimension, although lesser amounts of maximal medium (≥1.0 mm, ≤3.0 mm; N = 4 vessels) and coarse (>3.0 mm; N = 10 vessels) temper inclusions also occur. These particles range up to 4.10 mm and 6.20 mm.

In at least seven vessels, the quartz and other constituents seem to be associated with magnetite, which may have been a portion of an aggregate rock type that also included the quartz and some of the other mineral constituents. Only one vessel, 19, exhibits predominant magnetite and "other" temper (30–40%) with a lesser amount of quartz (20–30%). This vessel also has subrounded to rounded temper constituents, implying its origin as a sand. At least four to six other vessels have subrounded constituents, but most of the quartz and "other" constituents seem to have been derived from various crushed rocks and represent "grit" temper; thus the temper was likely derived from a combination of sand and grit in some cases, and more exclusively grit in other cases.

Other temper constituents include grog (crushed sherd), limestone, or possibly some other carbonate material, and muscovite mica. One vessel, 28, also contains 2–5% readily visible, fine to medium-sized garnets. The 25 grog-tempered vessels have mostly fine-sized grog, less than 1.0 mm in all cases, with occasional maximal medium (N = 10 vessels) and coarse (N = 1 vessel) constituents, ranging up to 3.10 mm. Grog constitutes less than 10% of the total paste in most cases (N = 16 vessels), but can comprise up to 10–20% (N = 5 vessels) and 20–30% (N = 4 vessels) of the paste.

Grog temper is not readily visible without magnification in most of the vessels (approximately 21) because it is generally too fine and sparse. The limestone temper was inferred from the occasional presence of a white, angular constituent and angular vesicles in the vessel pastes. The limestone temper has been eroded or leached away in many cases. It clearly does not represent shell temper as known from elsewhere in the Lesser Antilles and the Bahamas (e.g., Bullen and Bullen, 1972:144; Goodwin, 1979:241; Sears and Sullivan, 1978). Evidence that the whitish temper is not kaolin, as documented on St. Kitts (Goodwin, 1979:242), or volcanic tuff, as documented elsewhere (e.g., Petersen and Watters, 1988:178), is provided by its limestone-like eroded condition.

←

5 rim sherd showing smoothed finish. E. Exterior surface of vessel 6 body sherd showing burnished finish, and coil fracture on upper edge. F. Exterior surface of vessel 9 body sherd showing slipped and burnished finish. G. Interior surface of vessel 9 body sherd showing scraped finish and plastic flow. H. Interior surface of vessel 23 body sherd showing smoothed finish.

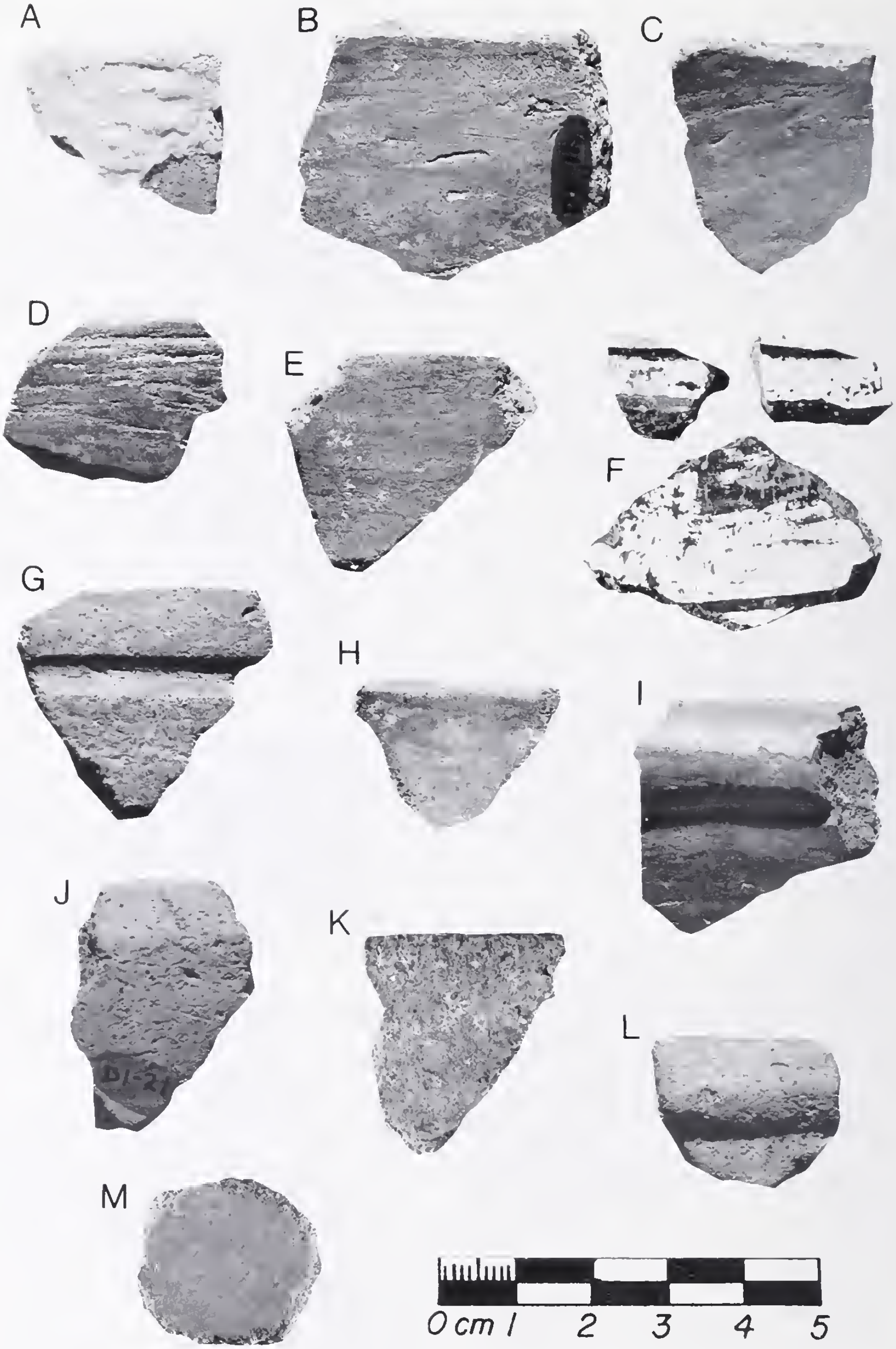

Fig. 7.—Amerindian ceramics from Fountain Cavern. A. Exterior surface of vessel 1 rim sherd showing carbonate encrustation. B. Interior surface of vessel 8 body sherd showing slipped and burnished finish, and coil fracture on upper edge. C. Exterior surface of vessel 10 body sherd showing smoothed finish, and coil fracture on upper edge. D. Exterior surface of vessel 11 rim sherd showing slipped and

The limestone temper is fine-sized in all cases and constitutes less than 10% of the paste in 15 of the 23 vessels where it is present. The fine-sized particles occur with lesser amounts of maximal medium (N = 14 vessels) and coarse (N = 5 vessels) particles in some vessels, ranging up to 3.8 mm, 4.30 mm, and 6.5 mm. This carbonate temper also occurs in larger amounts, 10–20% (N = 5 vessels), and 20–30% (N = 3 vessels) in some cases.

Muscovite mica, which is always fine-sized (<1.0 mm) and represents less than 10% of the paste, also occurs in at least six vessels. The mica may be an incidental inclusion in the paste, however, either from untempered clay, or derived from some coarser aggregate in conjunction with quartz and/or some other mineral temper.

The sum of these temper types suggests that some, if not most of the 29 defined vessels were not manufactured on Anguilla, or were made there using non-local clays and/or temper sources. In either case, these vessels likely reflect some degree of social interaction between islands in the West Indies, whether between Anguilla and the Lesser Antilles and/or the Greater Antilles. The "other" temper constituents almost certainly originated on one of the volcanic or composite islands, such as St. Kitts or St. Martin, and the quartz and magnetite likely had a similar origin. In particular, vessel 19, one of only two decorated vessels in the sample, exhibits a combination of subrounded or rounded quartz and black mineral sand, which appears nearly identical to temper in ceramics studied in several collections from volcanic islands (Petersen and Watters, 1988). Also, it was the presence of volcanic minerals that caused the failure of thermoluminescence dating in two sherds from Fountain Cavern. Geological studies are necessary to identify potential sources of such temper constituents on volcanic and composite islands.

Although precise temper data from the Lesser Antilles are rare, ceramic tempers from St. Kitts, particularly paste classes 1 and 3 (Goodwin, 1979:238–244) and others from Antigua (Hoffman, 1979), Grenada (Bullen, 1964:48) and St. Vincent (Bullen and Bullen, 1972:130–131, 142; Kirby, 1974:61), are only generally similar to those reported here. However, the sparse evidence on temper and paste is not necessarily comparable among Antillean studies. More detailed data from Martinique (Gauthier, 1974; Mattioni, 1982:6–17; Schvoerer et al., 1985) are likewise difficult to compare with the Fountain Cavern data, but again support the likely origin of at least some of the Fountain Cavern temper on a volcanic island. A recent petrographic thin section analysis of Amerindian ceramic samples from four islands in the northern Lesser Antilles also implies interisland interaction, especially the volcanic temper associations at Rendezvous Bay on Anguilla and Cupecoy Bay on St. Martin (Donahue et al., 1990:251).

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burnished, somewhat irregular finish. E. Exterior surface of vessel 12 rim sherd showing burnished finish. F. Exterior surfaces of three vessel 17 body sherds showing slipped and burnished finish, and white painted geometric decoration. G. Exterior surface of vessel 19 rim sherd showing slipped and smoothed finish, and incised decoration. H. Exterior surface of vessel 21 rim sherd showing smoothed finish. I. Interior surface of vessel 22 rim sherd showing slipped and burnished finish, and additive coil on interior edge of lip. J. Interior surface of vessel 23 rim sherd showing smoothed finish. K. Exterior surface of vessel 25 rim sherd showing slipped and smoothed finish. L. Interior surface of vessel 28 rim sherd showing slipped and smoothed finish, and additive coil on interior edge of lip. M. Exterior surface of cut ceramic disk showing slipped and burnished original finish.

Table 1.—*Fountain Cavern ceramic vessel attributes.*

Vessel designation (Number of specimens)	1 (1*)	2 (2)	3 (15)	4 (20)	5 (11)	6 (7)	7 (8)	8 (40)	9 (75)	10 (2)
Temper										
Quartz	×	×	×	×	×	×	×	×	×	×
Grog	×	×	×	×		×	×	×	×	×
Limestone	×	×	×	×	×	×	×	×		×
Magnetite		×	×	×					×	
Muscovite mica			×	×	×					
Other	×	×	×	×		×			×	
Texture										
Fine body	×	×	×	×	×	×	×	×	×	×
Medium body										
Extrusive	×	×	×	×	×	×	×		×	
Not extrusive								×?		×?
Moderate consolidation										
Thorough consolidation	×	×	×	×	×	×	×	×	×	×
Blocky angular fractures	×	×	×	×	×	×	×	×	×	×
Blocky platey fractures										
Manufacture										
Coiled	×	×	×	×	×	×	×	×	×	×
Unknown										
Mean coil size (mm)	11.70 ×7.40	12.15 ×9.00	10.00 ×8.63	9.50 ×6.98	12.10 ×8.55	11.75 ×9.20	9.20 ×8.45	10.05 ×6.20	10.55 ×7.80	12.00 ×6.85
Surface finish										
Smoothed exterior	×		×		×					×
Burnished exterior		×		×		×	×	×	×	
Slipped exterior				×			×	×	×	
Smoothed lip	×		×		×					×
Burnished lip		×		×		×	×	×		
Slipped lip										
Unknown lip									×	
Smoothed interior	×	×	×		×	×			×	
Burnished interior				×		×	×	×		×
Slipped interior							×	×		
Scraped interior		×			×				×	

* Additional specimens curated by the Anguilla Archaeological and Historical Society.

Table 1.—*Continued.*

Vessel designation (Number of specimens)	11 (3)	12 (2)	13 (2)	14 (2)	15 (2)	16 (2)	17 (4)	18 (4)	19 (1)	20 (3)
Temper										
Quartz	×	×	×	×	×	×	×	×	×	×
Grog		×	×			×	×	×	×	×
Limestone	×		×	×	×					×
Magnetite									×	
Muscovite mica		×		×		×				
Other				×	×	×	×	×	×	×
Texture										
Fine body	×	×	×	×	×	×	×	×		×
Medium body									×	
Extrusive					×		×		×	
Not extrusive	×?	×?	×?	×?		×?		×?		×?
Moderate consolidation					×					
Thorough consolidation	×	×	×	×		×	×	×	×	×
Blocky angular fractures	×	×	×	×			×	×	×	×
Blocky platey fractures					×	×				
Manufacture										
Coiled	×	×	×	×		×	×	×	×	
Unknown					×					×
Mean coil size (mm)	9.90 ×8.75	12.20 ×7.25	10.35 ×8.15			7.05 ×6.35	11.30 ×8.40	11.40 ×8.10	12.65 ×12.10	
Surface finish										
Smoothed exterior			×		×	×			×	
Burnished exterior	×	×		×			×	×		×
Slipped exterior	×						×	×	×	×
Smoothed lip			×		×	×			×	
Burnished lip	×	×		×				×		×
Slipped lip								×	×	×
Unknown lip							×			
Smoothed interior			×		×	×			×	
Burnished interior	×	×		×			×	×		×
Slipped interior	×							×		×
Scraped interior										

Table 1.—*Continued.*

Vessel designation (Number of specimens)	21 (1)	22 (1)	23 (13)	24 (3)	25 (1)	26 (1)	27 (5)	28 (1)	29 (2)
Temper									
Quartz	×	×	×	×	×	×	×	×	×
Grog	×	×	×	×	×	×	×	×	×
Limestone	×	×	×	×	×	×	×	×	×
Magnetite						×			×
Muscovite mica									
Other	×		×	×			×	×	×
Texture									
Fine body	×	×		×	×	×		×	×
Medium body			×				×		
Extrusive			×	×	×		×		
Not extrusive	×?	×?				×?		×?	×?
Moderate consolidation	×		×		×		×		
Thorough consolidation		×		×		×		×	×
Blocky angular fractures	×	×	×	×	×	×	×	×	×
Blocky platey fractures									
Manufacture									
Coiled			×	×	×	×	×	×	×
Unknown	×	×							
Mean coil size (mm)			12.20 ×7.80	10.70 ×6.75		9.30 ×7.80	11.00 ×7.70	12.15 ×6.70	9.80 ×9.15
Surface finish									
Smoothed exterior	×		×		×		×	×	
Burnished exterior		×		×		×			×
Slipped exterior		×		×	×	×		×	×
Smoothed lip	×		×		×		×	×	
Burnished lip		×		×		×			
Slipped lip		×		×	×	×		×	
Unknown lip									×
Smoothed interior	×		×		×		×	×	
Burnished interior		×		×		×			×
Slipped interior		×				×		×	
Scraped interior									×

Texture

The textural attributes for the 29 vessels include predominant pastes with a fine body (N = 26 vessels), and a few medium-bodied exceptions (N = 3 vessels) (Table 1). Consolidation was thorough to very thorough; only four vessels had moderate or less complete consolidation. Temper is extrusive from the surfaces on 15 vessels, particularly on the lower interior surfaces; the remaining vessels have little or no extrusive temper due to the apparently thorough degree of consolidation. Blocky angular fractures occur on 27 vessels; the other two have blocky platey fractures that reflect structural laminations and less complete consolidation. Structural laminations are present in various other vessels as well (Fig. 8B–D).

Manufacture

The presence of coil fractures confirms that coiling was employed to manufacture 25 of the 29 vessels. Although they are present, the coil fractures are indistinct in most cases (Table 1; Fig. 4D, 5C, 6E, 7B, C). Coiling cannot be verified for the other four vessels because they lack evident coil fractures. Mean coil dimensions for individual vessels were relatively small, ranging from 7.05–12.65 mm in height and 6.35–12.10 mm in thickness. Mean coil height and thickness for the entire sample (N = 23) are 10.83 mm and 8.00 mm, respectively (N = 23 vessels).

Surface Finish

A near even mix of smoothed (N = 13 vessels) and burnished (N = 16 vessels) exterior surfaces reflects a limited range of surface finish attributes (Table 1; Fig. 4–7), as these are closely related techniques (cf. Rye, 1981:89–90). An exterior slip was applied on at least 14 of the burnished vessels and one of the smoothed vessels (Fig. 6B, F, 7D, F, G, K). Slip thickness on six vessels shows a limited range from 0.05 mm to 0.15 mm. On the lip surface, 13 vessels exhibit smoothing and 13 burnishing; the other three vessels lack rim sherds. On interior surfaces, 14 vessels exhibit smoothing, 14 burnishing, and one both smoothing and burnishing. An interior slip was applied on at least seven of the burnished vessels and one of the smoothed vessels (Fig. 5A, 7B, I, L). Interior scraping, which is evident in at least four vessels towards the lower neck and/or body areas (Fig. 6G), may merely reflect incomplete smoothing or burnishing on the lower interior surfaces of some vessels.

Vessel Morphology

Few morphological attributes are available for this fragmentary sample, except for rim and lip attributes (Table 2; Fig. 9, 10). Two vessels exhibit square lips, two have pointed lips, and 22 rounded lips; three vessels lack preserved rims. One, likely two, vessels have incurvate rims, at least 18 vessels exhibit excurvate rims, and eight or nine do not preserve enough rim to determine this attribute. At least 12 vessels also have a thickened lip, which was achieved with an additional portion of a coil, or whole coil variably affixed to the uppermost portion of the interior of the rim (Fig. 4B, 5A, 7I, L). This thickened lip form is typical of post-Saladoid ceramics in the northern Lesser Antilles, for example, the Marmora Bay complex, ca. A.D. 900–1200, on Antigua (Hoffman, 1979; Rouse, 1974, 1976: 36).

Two vessels, 1 and 2, seem to have been incurvate cylindrical bowls, at least one of which had a flat bottom (Fig. 9, vessels 1 and 2). Another vessel, not

Table 2.—*Fountain Cavern ceramic vessel attributes, Munsell color designation key listed below.*

Vessel designation (Number of specimens)	1 (1)	2 (2)	3 (15)	4 (20)	5 (11)	6 (7)	7 (8)	8 (40)	9 (75)	10 (2)
Morphology										
Square lip	×									
Rounded lip		×	×	×	×			×		×
Pointed lip						×	×			
Unknown lip									×	
Incurvate rim	×?	×								
Excurvate rim			×	×	×	×	×	×		×
Unknown rim									×	
Thickened lip			×	×		×	×			×
Unthickened lip	×	×			×			×		
Unknown lip									×	
Hypothetical bowl	×	×	×?	×?	×					
Unknown vessel						×	×	×	×	×
Flat base		×							×	
Pedestaled base					×					
Metrics (mm)										
Lip	7.00	8.40–10.10	6.20	6.10	7.30–7.55	5.10	4.95–5.05	4.60		6.30
1 cm below lip	7.40	8.70–10.0	9.70	6.30	8.50–8.60	8.65	6.10	5.75–5.90		9.70
Neck		9.70–10.00	8.20–9.65	6.60–6.70	9.15–10.05	7.60	5.05–5.35	7.05–8.05		6.30–6.80
Body			7.45–10.05	6.05–8.55	8.55–13.15	6.90–12.55	4.85–8.50	5.45–9.55	5.10–10.05	6.70–6.85
Base		12.40–18.10			6.60–18.90				7.50–13.85	
Oral diameter (cm)		30			34			18		
Color (see below)			26							
Exterior	34	68	67	74	73	73	34	73	17*/97	62
Interior	68	68	67	67	73	73	34	73	129	35
Core	39	137	132	67	132	137	132	137	129	127
Firing cloud		132		42			41	70		

Table 2.—*Continued.*

Vessel designation (Number of specimens)	1 (1)	2 (2)	3 (15)	4 (20)	5 (11)	6 (7)	7 (8)	8 (40)	9 (75)	10 (2)
Firing										
Oxidized environment	×	×	×	×	×	×?	×?	×	×	×
Reduced environment										
Fast cooling		×	×			×	×	×		×
Slow cooling				×	×					
Unknown cooling	×								×	
Decoration										
None observed	×	×	×	×	×	×	×	×	×	×
Incision										
White-on-red										
Unknown										

17—red (10 R 4/6); 23—dark red (10 R 3/6); 33—reddish brown (2.5 YR 5/4); 34—red (2.5 YR 5/6); 35—red (2.5 YR 5/8); 38—reddish brown (2.5 YR 4/4); 39—red (2.5 YR 4/6); 41—very dark gray (2.5 YR 3/0); 44—dark red (2.5 YR 3/6); 62—reddish yellow (5 YR 6/6); 64—gray (5 YR 5/1); 67—reddish brown (5 YR 5/4); 68—yellowish red (5 YR 5/6); 70—dark gray (5 YR 4/1); 73—reddish brown (5 YR 4/4);74—yellowish red (5 YR 4/6); 88—reddish yellow (7.5 YR 7/6); 96—brown (7.5 YR 5/2); 97—brown (7.5 YR 5/4); 100—dark gray (7.5 YR 4/0); 101—brown/dark brown (7.5 YR 4/2); 102—brown/dark brown (7.5 YR 4/4); 104—very dark brown (7.5 YR 3/0); 109—white (10 YR 8/2); 127—grayish brown (10 YR 5/2); 129—yellowish brown (10 YR 5/4); 132—dark gray (10 YR 4/1); 133—dark grayish brown (10 YR 4/2); 137—very dark gray (10 YR 3/1).

* On slipped surface.

Table 2.—*Continued.*

Vessel designation (Number of specimens)	11 (3)	12 (2)	13 (2)	14 (2)	15 (2)	16 (2)	17 (4)	18 (4)	19 (1)	20 (3)
Morphology										
Square lip									×	
Rounded lip	×	×	×	×	×	×		×		×
Pointed lip										
Unknown lip							×			
Incurvate rim										
Excurvate rim	×	×						×	×?	×
Unknown rim			×	×	×	×	×			
Thickened lip								×		
Unthickened lip	×	×	×	×	×	×			×	×
Unknown lip							×			
Hypothetical bowl										
Unknown vessel	×	×	×	×	×	×	×	×	×	×
Flat base										
Pedestaled base										
Metrics (mm)										
Lip	5.95–6.75	6.00–6.55	7.75	6.70	4.75	5.95–6.50		4.50–4.55	11.00–11.25	5.80–6.25
1 cm below lip	8.30–8.70	6.60–7.25	8.50	7.30	6.20	6.45–7.05		8.50	12.05–12.20	7.15–8.20
Neck	7.85–9.05							6.45	12.30	
Body			8.05–8.25				7.55–8.20	6.10–8.05		
Base										
Oral diameter (cm)	24	24							26	
Color (see below)										
Exterior	67	34	34	39	133	133	109*/ 23*	88	17*	88
Interior	38	97	34	39	132	127	97	88	97	73
Core	127	96	132	41	137	127	104	41	100	67
Firing cloud										

Table 2.—*Continued.*

Vessel designation (Number of specimens)	11 (3)	12 (2)	13 (2)	14 (2)	15 (2)	16 (2)	17 (4)	18 (4)	19 (1)	20 (3)
Firing										
Oxidized environment	×	×	×	×			×	×?	×	×
Reduced environment					×	×				
Fast cooling	×		×	×			×	×	×	
Slow cooling		×?				×				
Unknown cooling					×					×
Decoration										
None observed	×	×	×	×	×	×		×		×
Incision							×		×	
White-on-red							×			
Unknown										

Table 2.—*Continued.*

Vessel designation (Number of specimens)	21 (1)	22 (1)	23 (13)	24 (3)	25 (1)	26 (1)	27 (5)	28 (1)	29 (2)
Morphology									
Square lip									
Rounded lip	×	×	×	×	×	×	×	×	
Pointed lip									
Unknown lip									×
Incurvate rim									
Excurvate rim	×?	×	×	×		×		×	
Unknown rim					×		×		×
Thickened lip		×	×	×	×	×		×	
Unthickened lip	×						×		
Unknown lip									×
Hypothetical bowl			×						
Unknown vessel	×	×		×	×	×	×	×	×
Flat base			×						
Pedestaled base									
Metrics (mm)									
Lip	5.50–5.90	6.00–6.25	6.55	7.25–7.75	5.20–5.55	5.40–5.60	6.25–6.80	5.05–5.40	
1 cm below lip	6.05	9.10	11.70–11.80	10.05–10.65	8.05–8.25	7.80–8.05	7.35	6.50–6.65	
Neck	6.75	6.70–7.35	8.80–9.60	5.75–6.35	7.00–7.45	6.10		4.90–5.35	
Body			7.05–14.90	5.90–7.25			6.35–7.80		6.65–10.00
Base			9.90–18.95						
Oral diameter (cm)		22	28	26					
Color (see below)									
Exterior	68	44*	68	39*	38*	44*	68	39*	39*
Interior	68	44*	67	33	102	44*	101	73	97
Core	64	73	68	97	129	68	70	132	132
Firing cloud									

Table 2.—*Continued.*

Vessel designation (Number of specimens)	21 (1)	22 (1)	23 (13)	24 (3)	25 (1)	26 (1)	27 (5)	28 (1)	29 (2)
Firing									
Oxidized environment	×	×	×	×	×	×	×?	×?	×
Reduced environment									
Fast cooling	×		×				×	×	
Slow cooling				×?		×?			×
Unknown cooling		×			×				
Decoration									
None observed	×	×	×	×	×	×	×	×	×
Incision									
White-on-red									
Unknown									

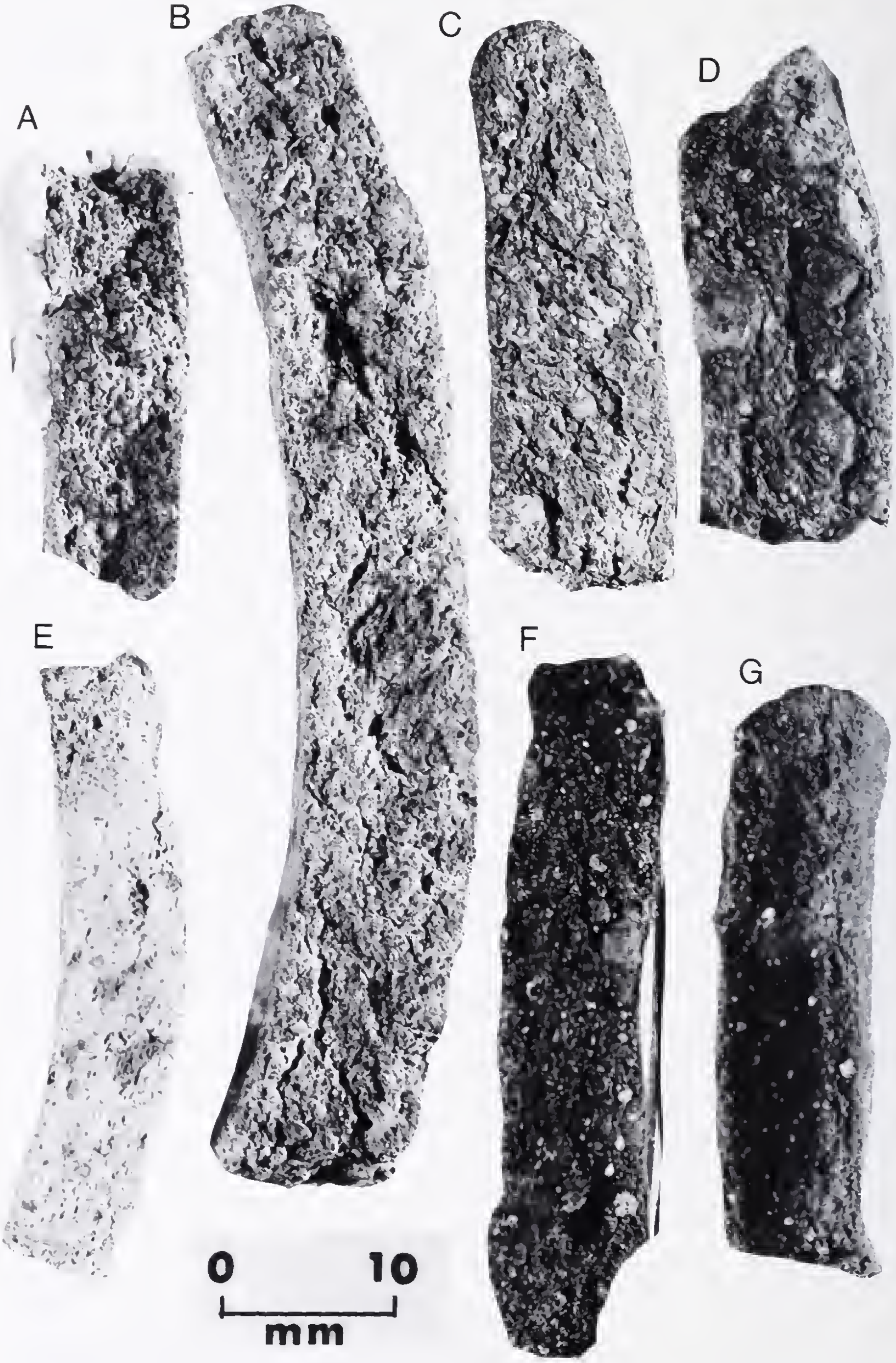


Fig. 8.—Amerindian ceramic sherd cross sections on broken edges showing temper constituents and internal laminations. A. Cross section of vessel 1 rim sherd showing quartz, grog, limestone and other temper constituents, and carbonate encrustation on outer surfaces. B. Cross section of vessel 2 rim

included in this study, was reconstructed by the AAHS from about 50 surface-collected sherds in Fountain Cavern. Photographs and a general description provided by the AAHS (Douglas, personal communication, 1991) establish that this vessel is a cylindrical flat-bottomed bowl with a sharply incurvate upper body, namely a "cazuela" (Fig. 11; also figured in Douglas, 1986*b*:37). Incurvate or "cazuela" vessels seem to be a typical late vessel form in the regional sequence throughout the West Indies, occurring, for example, in the Marmora Bay complex and Caliviny or Troumassoid series developments after ca. A.D. 900 (e.g., Boomert, 1987:22–24; Bullen, 1962, 1964:48–49; Bullen and Bullen, 1972:142; Krieger, 1931: plate 6; Rouse, 1974:174).

Some other vessels may have been cylindrical jars, although many of these vessels more likely were bowls. There is little other evidence of body morphology, however. One other vessel (Fig. 9, vessel 9) has a flat bottom like vessel 2 (Fig. 9) and another vessel, 23, has a pedestaled flat bottom (Fig. 4C, 10, vessel 23). The latter may well have been a bowl. Three other partially restored vessels, again not included in this study, which were assembled from AAHS surface-collected sherds, have been described by Douglas (personal communication, 1991) as two elongate "jugs" and a "double gourd" form.

Amerindian ceramic vessel forms have not been thoroughly reported from the Lesser Antilles, although a variety of complicated forms are known, particularly for the earlier Saladoid ceramics (e.g., Clerc, 1968; Mattioni, 1979, 1982; Mattioni and Nicolas, 1972; Petitjean Roget, H. 1978; Petitjean Roget, J., 1970). The Fountain Cavern vessel lip, rim, and base morphological attributes seem comparable to other ceramics from the Antilles, specifically those occurring later in the regional sequence (e.g., Bullen, 1964: fig. 3; Fewkes, 1922: fig. 63; Goodwin and Walker, 1975: fig. 1; Krieger, 1931: plates 7, 49, 52; Mattioni, 1976: plate 1; Wilson, 1989: table 2). Although these attributes mainly represent "unrestricted, simple" and "unrestricted, inflected" bowl forms, the AAHS "cazuela" vessel represents a "restricted, dependent, composite" bowl form (see Levin, 1980: fig. 2).

One unusual artifact is a vessel sherd (about 24.60 × 22.85 mm) that was apparently cut and possibly ground after breakage and thus represents the only recycled ceramic artifact from Fountain Cavern (Fig. 7M). It exhibits a red slip on both surfaces and may be a "gaming piece." Comparable examples of ceramic disks are known in the West Indies and nearby areas (e.g., Bullen, 1962:23, 32, 1964:20, plate XII.4–5; Bullen and Bullen, 1972: plate VI.e, XVIII.e; Pendergast, 1971:76).

Metrics

Minimum and maximum values for various metric categories are presented in Table 2. However, mean values, which are not available in Table 2, are presented here.

←

sherd showing quartz, grog, limestone, magnetite and other temper constituents, and structural laminations. C. Cross section of vessel 5 rim sherd showing quartz, limestone and mica temper, and structural laminations. D. Cross section of vessel 6 body sherd showing quartz, grog, limestone and other temper constituents, and structural laminations. E. Cross section of vessel 10 body sherd showing quartz, grog, limestone and other temper constituents. F. Cross section of vessel 17 body sherd showing quartz, grog and other temper constituents. G. Cross section of vessel 29 body sherd showing quartz, grog, limestone and other temper constituents.

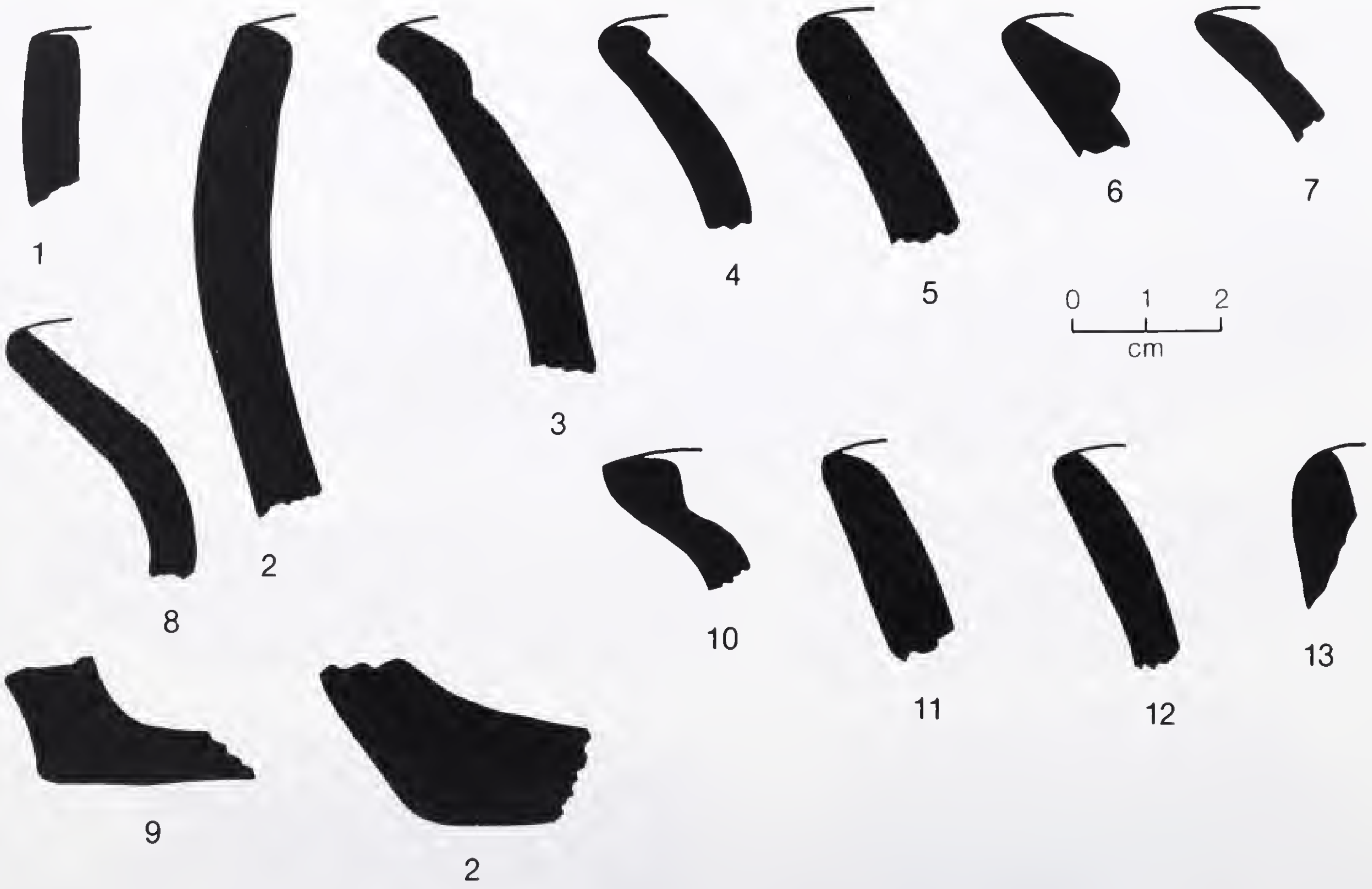


Fig. 9.—Rim and base profiles for Fountain Cavern ceramic vessels 1–13, as available. Numbers correspond to vessel designations.

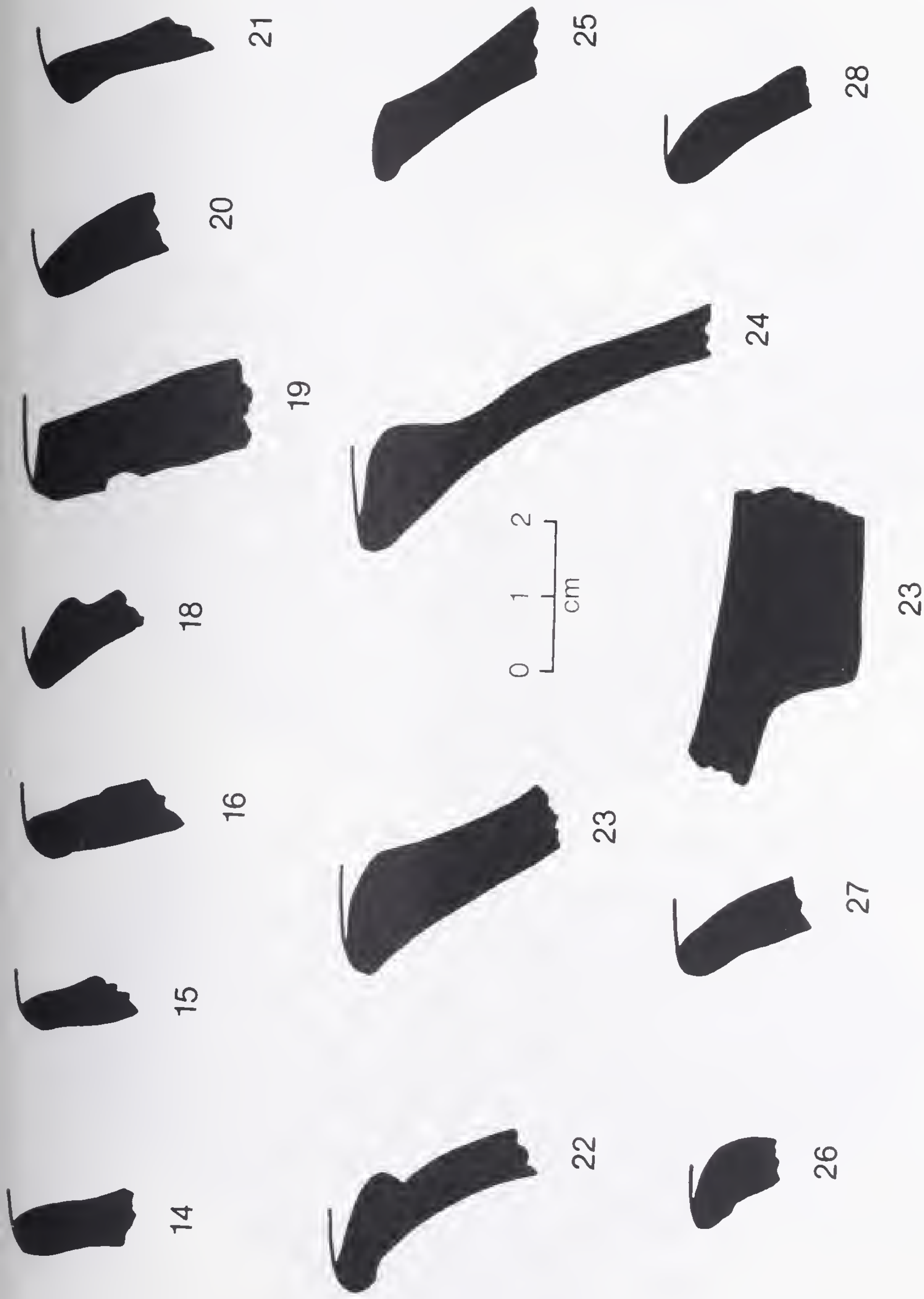
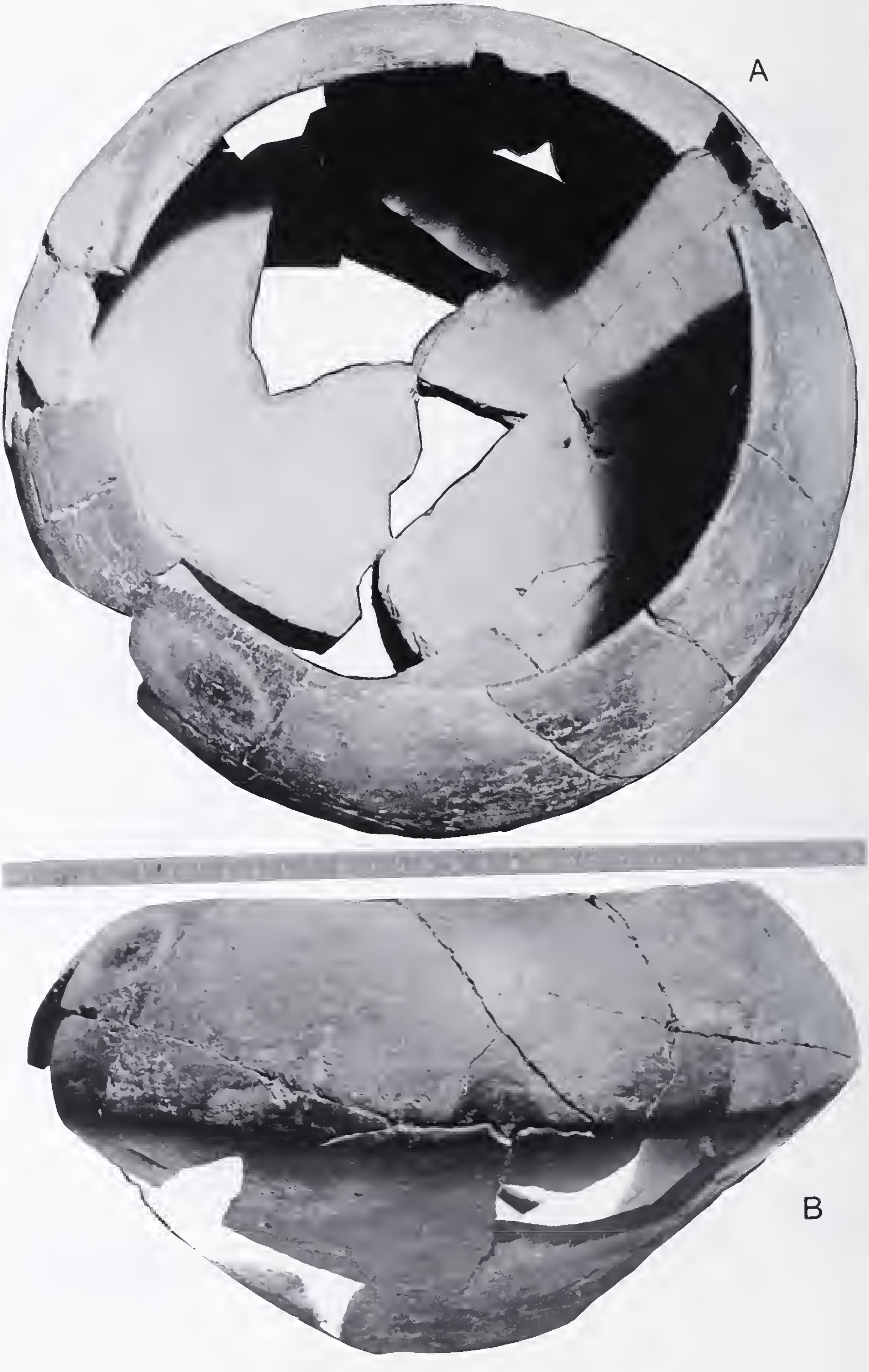


Fig. 10.—Rim and base profiles for Fountain Cavern ceramic vessels 14–29, as available. Numbers correspond to vessel designations.


A
B

Measurements of lip thickness and of thickness 1 cm below the lip provide the most readily available metric data for the sample given the fragmentary condition of all studied vessels. Mean values of 6.38 mm (N = 26) and 8.13 mm (N = 26) for the lip and 1 cm below the lip, respectively, indicate that most vessels have relatively thin upper rims. Likewise, mean values of 7.59 mm (N = 18) and 8.08 mm (N = 15) for neck and body thickness, respectively, corroborate the overall delicate nature of these vessels. Base thickness (mean = 13.24 mm; N = 4) confirms that vessels were thickest in their lowermost portions. Inferred oral diameter (mean = 25.8 cm; N = 10) establishes that the vessels were not particularly large. The ceramic cut disk is 8.40 mm thick.

Metrics for the four vessels partially restored by the AAHS (Douglas, personal communication, 1991) are as follows. The "cazuela" vessel: basal diameter, 9 cm; maximum body diameter, 30 cm; oral diameter, 20 cm. The two "jugs": basal diameters, 8 cm and 10 cm, and maximum body diameters, 40 and 45 cm, respectively; oral diameter, 20 cm. The "double gourd" form: basal diameter, 8.5 cm; maximum body diameter, 18 cm; oral diameter, 11 cm.

Color and Firing Attributes

The color attributes are the result of firing conditions, the clay source and in some cases, intentional slips and conditions of use, discard, and post-depositional alteration (Table 2).

Exterior colors range from a red (Munsell 10 YR 4/6) and dark red (10 YR 3/6) to white (10 YR 8/2) on slipped and painted surfaces, respectively. The most typical exterior values are red (2.5 YR 4/6) and yellowish red (5 YR 5/6) on slipped and unslipped surfaces, respectively. Interior colors range from reddish brown (2.5 YR 5/4) to dark gray (10 YR 4/1), with a most typical value of reddish brown (5 YR 4/4). The core colors range from red (2.5 YR 4/6) to very dark gray (10 YR 3/1), with a most typical value of reddish brown (10 YR 5/4) to dark gray (10 YR 4/1).

These values and the nature of the gradational change in the core color reflect a predominance of oxidized firing environments (N = 27 vessels, or 93%) and fast cooling (N = 16, or 55.2%) after firing. Seven vessels may have been slow cooled; cooling rate could not be determined for another six vessels. The majority of the vessels seem to contain carbon-rich clay. The sum of these attributes is generally similar to the few other comparable data available from elsewhere in the Antilles (e.g., Kirby, 1974; Petersen and Watters, 1988).

Decoration

A lack of decoration is most characteristic of the Fountain Cavern sample (Table 2). Only two vessels (6.9%), represented by only five sherds (0.6% of the total sample), have exterior decoration. One vessel, 17, was decorated with a white-on-red painted linear geometric motif on a red slipped background (Fig. 7F). The white elements, 4.90–11.25 mm wide, unfortunately are too small and broken to comprise an easily recognizable motif. A simple linear incision, about 1.15 mm wide, bounds one area of the white painted decoration. The other decorated vessel, 19, exhibits a single, deep, U-shaped exterior incision about 9.60 mm below the

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Fig. 11.—Restored ceramic vessel recovered from Fountain Cavern by the Anguilla Archaeological and Historic Society. A. Top view of vessel. B. Side view of vessel. (Photographs courtesy of Nik Douglas, AAHS.)

lip (Fig. 7G). The incision likely encircled the entire vessel exterior and is about 4.10 mm wide and 2.10 mm deep.

Vessel 17 bears classic white-on-red decoration and as such, may be indicative of Saladoid ceramics, ca. 200 B.C. to A.D. 600. However, white-on-red decoration persisted into the period ca. A.D. 600–900, as in the Mill Reef complex on Antigua. The latter includes linear and curvilinear motifs rather than just the curvilinear motifs characteristic of the earlier Indian Creek complex (Rouse, 1974, 1976). Unfortunately, vessel 17 is too incomplete to afford precise dating. The other relatively thick, broad-lined incised vessel, 19, seems to be attributable to a post-Saladoid temporal span, ca. A.D. 600–1200 or later, as are most or all of the undecorated vessels (e.g., Boomert, 1987; Bullen, 1962, 1964; Bullen and Bullen, 1972, 1976; Hoffman, 1979; Mattioni, 1979, 1982; Rouse, 1974, 1976; Wilson, 1989).

CERAMIC DISTRIBUTION

Although derived from very limited testing in Fountain Cavern, the ceramic sample is rather large in terms of vessel and sherd frequencies. However, this sample is limited when compared with the ceramic sample collected from the surface of Fountain Cavern by the AAHS before and after Watters' testing in 1986. A recounting of the previously collected ceramics, combined with a lesser number of Amerindian ceramics collected since 1986, increased the total number of prehistoric sherds from 5000–5500 to 6604. Douglas (personal communication, 1991) provided detailed information about the AAHS ceramic sample, from which the following summary is extracted.

All of the 6604 AAHS ceramics came from Chamber 1. Of the 6604 sherds, 10 specimens were found in Pool 1, 145 encrusted specimens (plus one brought by Watters to the U.S.) came from the water-filled cavity beside the pool, 55 came from the floor sloping toward Pool 1 from the level area beneath the entrance (by the ladder), and 6394 originated in close proximity to the large stalagmite (an area roughly equivalent to Watters' Surface Area A) (Fig. 3). Although a grid was not used by AAHS to collect the ceramics in a systematic manner, their general provenience information clearly establishes that the large majority (96.8%) were concentrated near the stalagmite with Petroglyph 12.

Twenty sherds exhibit some form of decoration on the exterior surface, including seven with white-on-red painting, a spiral-shaped handle with painting, and 12 with modeled decoration. Of the latter 12 specimens, two are adornos, one of which may depict a snake and the other possibly a snail. At least 5934 other specimens exhibit no decoration, while 650 others are too fragmentary or small to ascertain whether or not they were decorated. Thus, a total of as many as 6584 (99.7%) of the AAHS Amerindian ceramic sample may have been undecorated.

Also according to Douglas, of the 6604 sherds, at least 362 are vessel rims and five are griddle rims, 91 represent base sherds, two are adornos, and as many as 6144 are body sherds and fragments. Of the total rim sherds, 286 (79%) are "folded" (thickened) specimens, and of the base sherds all but one are concave to some degree. Four partially restored vessels were discussed above, but many more vessels (Douglas estimated 60–100 vessels) are probably represented in the AAHS collection. The four vessels exhibit a red slip on the exterior and an unmodified interior; the two "jugs" and the "double gourd" form exhibit carbon deposits solely on their lower interior surfaces.

Fountain Cavern can be expected to yield many more ceramics during future archaeological testing. The establishment of vessel lots, using the CMNH sample in particular, permits examination of vertical distribution of the Amerindian ceramics and thus permits assessment of disturbances in Fountain Cavern (Table 3; Fig. 3).

Vessel 1 is based on a single specimen associated with an unstudied sample of 145 encrusted sherds, likely constituting one or more currently unrestored vessels recovered from Surface Area B adjacent to Pool 1 by the AAHS (Watters, 1991). The other 145 encrusted specimens are included in the above summary derived from Douglas' information. Vessels 2–21 originated on the surface and deep within test pit 1, vessels 22–28 in and on the area of test pit 3, and vessel 29 in and on test pit 2. No admixture of vessels occurred between the test pits and surface areas, which is not surprising given the relatively great distance between them (see Fig. 3). However, admixture is obvious within each of the two deeper test pits, 1 and 3. For example, specimens attributable to vessel 9 were recovered on or near the surface and in sectors A, B, and C of test pit 1, in levels 0–10 cm, 5–50 cm, 31–40 cm, 35–50 cm, and 90–100 cm. Likewise, specimens attributable to vessel 23 were found in the 0–10 cm, 11–20 cm, and 21–30 cm levels of test pit 3. These and other examples document considerable admixture in Fountain Cavern, at least in the tested areas. It seems probable that various taphonomic factors, especially human trampling and shifting of rocks, have caused downward movement of cultural remains through the cave deposits. Watters (1991) discusses in detail how the cultural remains, including modern artifacts, have migrated downward through crevices and holes among the rocks in test pit 1. In test pit 3, the deposits may have been more substantially disturbed through various historic activities including the installation of the steel access ladder in the cavern in 1953.

Overview

The ceramic sample from Fountain Cavern is attributable to one or possibly several late prehistoric components; it is quite possibly restricted to a relatively brief time span, at least for most of the vessels. These vessels very likely represent ritual deposits in Fountain Cavern, almost certainly connected with the various petroglyph panels (Douglas, 1985, 1989), the antiquity of which has been variably estimated at ca. A.D. 900–1200, the post-Saladoid period (Dubelaar, 1989; Petitjean Roget, 1989).

The dense concentration of ceramics in test unit 1 and nearby Surface Area A, which were adjacent to the large, somewhat central "Jocahu" stalagmite (#12 in Douglas, 1989), supports this interpretation. The relative scarcity of elaborately modeled or otherwise decorated ceramics might be surprising if the ceramic vessels were brought to the cavern as ritual offerings. However, it is probable that the vessels were indeed typically little decorated, or undecorated and, as such, still may well have been "worthy" ritual objects themselves or they contained "worthy" offerings of some sort. Indeed, in general, post-Saladoid ceramics throughout the northern Lesser Antilles often were left undecorated or "plain." The fragmented condition of the vessels could be due to several factors, including intentional breakage by the Amerindians, as part of their ceremonies; or by historic visitors, to destroy pagan idols; unintentional breakage by either group; or breakage by natural causes such as rock falls from the cavern roof.

Amerindian ceramics have been previously recovered from varied contexts in other closed sites in the West Indies, particularly in the Greater Antilles, and

Table 3.—*Distribution of defined ceramic vessel lots by provenience in Fountain Cavern.*

General provenience	Code number[a]	Vessel designation														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Surface Area A	D1-1				1											
Surface Area B	D1-2		2													
Pool 1	D1-25	1														
Test pit 1, Sector A, 0–10	D1-3					2		2	1							
Test pit 1, Sector A, 10–20	D1-4			2	8	2			4							
Test pit 1, Sector A, 20–30	D1-5				4	2	5	5	2							
Test pit 1, Sector A, 30–70	D1-6				1					7						
Test pit 1, Sector B, 0–5	D1-7			2	2				4							1
Test pit 1, Sector B, 5–35	D1-8			11	4		2		21	47	2	3	2	2	2	1
Test pit 1, Sector B, 35–50	D1-9									1						
Test pit 1, Sector C, 0–5	D1-10					3			3	5						
Test pit 1, Sector C, 5–50	D1-11					2			5	10						
Test pit 1, 90–100	D1-12									5						
Test pit 1, 100–110	D1-13															
Test pit 1, 110–120	D1-14							1								
Test pit 2, 0–10	D1-19															
Test pit 3, Surface	D1-20															
Test pit 3, 0–10	D1-21															
Test pit 3, 10–20	D1-22															
Test pit 3, 20–30	D1-23															
Totals		1	2	15	20	11	7	8	40	75	2	3	2	2	2	2

[a] CMNH catalogue numbers; D1-15, -16, -17, -18, -24 and -26 did not include ceramic specimens assigned to vessels.

Table 3.—*Continued.*

General provenience	Code number[a]	Vessel designation														Totals
		16	17	18	19	20	21	22	23	24	25	26	27	28	29	
Surface Area A	D1-1															1
Surface Area B	D1-2															2
Pool 1	D1-25															1
Test pit 1, Sector A, 0–10	D1-3															5
Test pit 1, Sector A, 10–20	D1-4															16
Test pit 1, Sector A, 20–30	D1-5															18
Test pit 1, Sector A, 30–70	D1-6															8
Test pit 1, Sector B, 0–5	D1-7															9
Test pit 1, Sector B, 5–35	D1-8	2	1													100
Test pit 1, Sector B, 35–50	D1-9															1
Test pit 1, Sector C, 0–5	D1-10					1	1									13
Test pit 1, Sector C, 5–50	D1-11															17
Test pit 1, 90–100	D1-12			4		2										11
Test pit 1, 100–110	D1-13		3		1											4
Test pit 1, 110–120	D1-14															1
Test pit 2, 0–10	D1-19														2	2
Test pit 3, Surface	D1-20							1								1
Test pit 3, 0–10	D1-21								4							4
Test pit 3, 10–20	D1-22								4	2			4			10
Test pit 3, 20–30	D1-23								5	1	1	1	1	1		10
Totals		2	4	4	1	3	1	1	13	3	1	1	5	1	2	234

nearby areas. Although some of these finds are domestic refuse from subsistence activities, in other cases they clearly represent ceremonial deposits, including funerary urns and containers for ritual offerings (e.g., Brainerd, 1953; Borrell Bentz, 1979; De Booy, 1915; Fewkes, 1922:237–240; Harrington, 1979:271–273; Krieger, 1931:74–79; Lovén, 1979:123–125, 129; Pendergast, 1971; Rouse, 1948: 508; Veloz Maggiolo, 1972:157–166). These ceramics demonstrate the potentially varied roles for this form of material culture. At Fountain Cavern, ceramic vessels may have served to collect "drip water" used in ritual activities and to transport and present food, beverage or other offerings, and they may have served as funerary vessels, among a range of ceremonial functions. Fountain Cavern was almost certainly not a habitation site, and it contains a notable concentration of petroglyphs. Therefore, a ceremonial function for the ceramics seems to best explain their presence.

Some of the sherds may be the remains of vessels broken during non-ritual activities, such as water collecting from Fountain Cavern, particularly from Pool 1. Historically, Fountain Cavern was a known permanent source of water even in times of severe drought; it may have been known as such to the Amerindians as well, assuming it contained water during prehistoric time.

In any case, all of the vessels (except possibly vessel 17) are attributable to a post-Saladoid component or components, ca. A.D. 600–1200, and quite possibly ca. A.D. 900–1200, or later. These cross dates are based on the correspondence between the Fountain Cavern sample and the incompletely reported Marmora Bay complex on Antigua as well as the unreported Rendezvous Bay (AL2) and Sandy Ground (AL3) sites on Anguilla that are radiocarbon dated generally to after ca. A.D. 500–600. In particular, these entities share common usage of a typical red slip, a near absence of decoration, "folded" or "thickened" rims produced "by adding a cylindrical coil of clay" and minor usage of white-on-red painted and broad-lined incised decoration (e.g., Rouse, 1974:175–176, 1976:36–37; see also Davis, 1988). Rouse (1976:39–40, 1982:50, various) and other scholars have related these and similar ceramics elsewhere in the Lesser Antilles to the Elenoid ceramic series of the Virgin Islands and eastern Puerto Rico, with more distant relationship to the Ostionoid ceramic series of western Puerto Rico and the Dominican Republic and widespread correlates farther west in the Greater Antilles (e.g., Bullen and Bullen, 1976:5; Goodwin and Walker, 1975:86; Lee, 1978; Rouse, 1964:11; Sears and Sullivan, 1978:14; Veloz Maggiolo, 1972:102; Wilson, 1989:430–431). Rouse (1986:143–144) now includes the northern Lesser Antilles post-Saladoid ceramics within his Elenan Ostionoid subseries, first defined in the eastern Greater Antilles.

Some archaeologists question the applicability of the Elenoid series (Elenan Ostionoid subseries) designation over such a broad area and without more detailed definition (e.g., Goodwin, 1979:305; Watters, 1980:274). Post-Saladoid ceramics known from elsewhere in the Antilles share general similarities in morphology and surface finish with the Fountain Cavern specimens, including, for example, Magens Bay ceramics of the Virgin Islands (Bullen, 1962:13, 59–63) and Caliviny or Troumassoid or later ceramics of Barbados, Grenada, St. Vincent, the Grenadines, and Martinique (e.g., Boomert, 1987:21–27; Bullen, 1964: Bullen and Bullen, 1972:48–50, 160–167, table 8; Kirby, 1974; Mattioni and Bullen, 1970; Petitjean Roget, 1978). One or more likely several widespread ceramic horizon styles can be postulated in the region during the post-Saladoid period on the basis of these similarities. However, these correlations are tentative because the available ceramic sample from Fountain Cavern does not completely match any other sample previously reported in the Antilles, particularly for the temper attributes. A more expansive treatment of post-Saladoid ceramics from Anguilla is planned once the analysis of samples from two open sites, Rendezvous Bay and Sandy Ground, has been completed.

As Goodwin (1979) has tentatively identified on St. Kitts, it seems likely that local, island-specific, and regional ceramic and broader cultural sequences will ultimately be discernible in the Lesser Antilles. Hence, precise correlation between different manifestations on different islands should not necessarily be expected in spite of apparently widespread horizon styles.

Interisland population interaction, specifically trade and exchange, seems quite likely to be at least one mechanism responsible for the general similarities among post-Saladoid ceramics and, in fact, has been long suggested, if largely unsubstantiated, in regional research (e.g., Boomert, 1987:195; Bullen, 1962:17; Bullen and Bullen, 1972; Daggett, 1980:149–150; Goodwin and Walker, 1975:87, 91; Mattioni, 1979:11; Rouse, 1976:39–40, 1977:9; Sears and Sullivan, 1978:11, 23; Veloz Maggiolo, 1972:108–120). As noted above, temper data for the available Fountain Cavern sample seem to document the presence of one, possibly many, nonlocal, "exotic" tempers, or more likely whole vessels which originated on one or another of the volcanic islands in the West Indies. Given this observation and other evidence of long distance social interaction during the long span of West Indian prehistory, future ceramic studies should be designed to address this significant issue in both local and regional contexts.

Acknowledgments

Members of the AAHS, who assisted in field research, and officials of the Government of Anguilla, who authorized research and export permits, are acknowledged in Watters' (1991) article. Funding was provided by the Canadian International Development Agency (to the Government of Anguilla), M. Graham Netting Research Fund (CMNH), Charles Cohn Foundation, and Eugene M. Grant. We are indebted to Nik Douglas for providing photographs of the ceramic vessel restored by the AAHS (Fig. 11) and information about the surface-collected ceramics. At CMNH, Stanley W. Lantz photographed most of the ceramics and Sylvia Keller patiently typed manuscript revisions. At the University of Maine at Farmington, Kara Ohlund and Ann Robinson produced and edited the tables, respectively. We gratefully acknowledge the geological expertise of Gary Laverdiere at the University of Maine at Farmington in verifying and refining Petersen's identifications of tempers.

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ANNALS OF CARNEGIE MUSEUM
Vol. 60, Number 4, Pp. 359-363 27 November 1991

A NEW AULOSTEGID (BRACHIOPODA: AULOSTEGOIDEA) FROM THE LOWER MISSISSIPPIAN OF NORTHCENTRAL IOWA

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Abstract

Archaiosteges harperi, n. gen. n. sp., is the earliest known representative of the superfamily Aulostegoidea. It occurs in the early Osagean (late Middle or early Upper Tournaisian) Gilmore City Formation ("Humboldt Oolite") of northcentral Iowa. Internal morphology of the dorsal valve permits referral of this genus to the subfamily Echinosteginae of the family Aulostegidae.

Although there is some suggestion of postmortem abrasion, most specimens are well preserved, which indicates moderate predepositional transport. The sedimentary environments of this formation at this locality range from high-intertidal beach deposits to lagoonal infilling, implying that this species probably was adapted to a shallow water environment. There is little evidence that *A. harperi* had an attached mode of live as an adult.

Introduction

This paper is an addendum to one describing new brachiopod taxa from the Gilmore City Formation (Carter, 1983). In that paper I misidentified a single ventral valve of an enigmatic productid as *Pustula* sp. because I lacked information concerning the dorsal interior (Carter, 1983: table 1). New material from the same locality, including a number of dorsal valves and another small ventral valve, now allows confident identification and description of a new taxon from the Lower Mississippian of North America.

The beds from which the specimens were collected have been assigned variously to the Gilmore City Formation (Woodson and Bunker, 1989:14) or to the "Humboldt Oolite" (Brenckle and Groves, 1987:562). The latter authors have suggested from foraminiferal evidence that these beds are Lower (but not lowest) Osagean in age. Also, Woodson and Bunker (1989:6) point out that the name "Humboldt Oolite" was never formally proposed as a stratigraphic unit. However, its informal usage is succinct and there is some paleontological evidence (Brenckle and Groves, 1987) that these beds are significantly younger than those at the type section of the Gilmore City Formation to the west.

All of the specimens came from the upper part of the section at the well known Hodge's P & M—Martin Marietta Quarry just northeast of the city of Humboldt, Humboldt County, Iowa. These beds may represent a high-intertidal environment (Brenckle and Groves, 1987:563) and backshore beach deposits (Gerk and Levorson, 1982). The entire section at Hodge's Quarry is interpreted by Glenister and Sixt (1982:9) as a single shallowing upward sequence, culminating in evaporitic collapse breccias.

At least some of the productid specimens described here were recovered from the backshore beach coquinas discussed by Gerk and Levorson (1982). Most of the specimens give some indication of abrasion or even decortication but the

Submitted 11 January 1991.

preservation is generally good. In any case, it is very unlikely that any of the specimens were found in life position.

Brunton and Mundy (1988) suggested that, in general, aulostegoideans were adapted to an attached mode of life. However, no mode of attachment is ascertainable for this new species and a *modus vivendi* is not obvious. A cicatrix is not preserved and was probably not present on either of the two ventral valves available for study, and creeping adherent spines also seem to be lacking. The preserved spines are directed toward all of the margins.

Furthermore, there is no indication of a hard substrate for an attachment site in these Humboldt oolite sediments. The most likely possibilities for a hard substrate here are probably 1) bioherms, 2) large clasts, or 3) hardgrounds. Lower Carboniferous bioherms in North America are restricted to the carbonate shelf edge (Lane, 1982), which occurs far from this part of Iowa. The largest clasts at this locality in the Gilmore City Formation are biogenic and consist of rare large mobile snails (Harper, 1977), solitary corals (Carlson, 1964), and a few medium-sized brachiopods (Carter, 1983). It seems unlikely that this new genus would have been attached to any of these organisms. Hardgrounds are evidence of a sedimentary stillstand, for which there is no documentation in this part of the Gilmore City sedimentary sequence, although one may have been formed after the topmost evaporitic beds were deposited and before the collapse breccias were formed. Therefore, it is possible that this genus was attached only in its juvenile stage and lived freely as an adult.

SYSTEMATIC PALEONTOLOGY

The specimens described herein are deposited in The Carnegie Museum of Natural History (CM), Section of Invertebrate Paleontology. The suprageneric classification used here follows that of Cooper and Grant (1975).

Order Strophomenida Öpik, 1934
Suborder Productidina Waagen, 1883
Superfamily Aulostegoidea Muir-Wood and Cooper, 1960
Family Aulostegidae Muir-Wood and Cooper, 1960
Subfamily Echinosteginae Muir-Wood and Cooper, 1960
Genus ***Archaiosteges***, new genus

Type species.—*Archaiosteges harperi* n. sp.

Etymology.—From the Greek *archaios,* primitive, and *steges,* room (masculine).

Species assigned.—Type species only.

Diagnosis.—Small to medium-sized geniculate Echinosteginae with moderately developed trails and moderately thin body cavity; outline subquadrate; ears weakly produced; ventral interarea moderately short, apsacline; dorsal interarea short, anacline; elytridium not preserved, possibly absent; ventral valve ornament of concentric rugae and spine-bearing tubercles only; spines of one size only, probably suberect; dorsal interior with large quadrilobate cardinal process; marginal rim well developed.

Description.—Same as for the type species given below.

Age.—Lower Osagean (late Middle or early Upper Tournaisian).

Comparisons.—This new genus is not closely similar to any described genus of the Echinosteginae. It is most similar to the genera *Echinosteges* Muir-Wood and Cooper, 1960, and *Edriosteges* Muir-Wood and Cooper, 1960, both of Permian age. *Archaiosteges* differs from both of these genera in having a dorsal interarea, a geniculate ventral valve, a modestly raised dorsal adductor platform, and in lacking a gutterlike flange around the ventral trail. In addition, it differs from *Echinosteges* in lacking a plicated trail. It also can be distinguished from *Edriosteges* in having a tuberculate rugose ornament.

Remarks.—Affinities of this new genus with the subfamily Echinosteginae are clearly indicated by the presence of a lophidium, quadrate cardinal process, nonspinose dimpled dorsal valve, and strongly dendritic posterior dorsal adductors raised on a low platform. It differs from all other members of this subfamily in having a short dorsal interarea, which is also well illustrated in the aulosteginine genus *Taeniothaerus* Whitehouse (Muir-Wood and Cooper, 1960: plate 11). Other workers (Cooper and Grant, 1975, and Brunton and Mundy, 1988) have suggested that a dorsal interarea was lacking in this superfamily. The presence of a dorsal interarea in two genera of this superfamily strengthens Cooper and Grant's (1975) assertion that the Aulostegoidea were derived from the Strophalosioidea, a group characterized by interareas in both valves.

The appearance of *Archaiosteges* in the late Middle or early Upper Tournaisian substantially extends the range of the superfamily Aulostegoidea. Previously, the earliest aulostegoideans were known only from the family Sinuatellidae (Brunton and Mundy, 1988) of Late Visean age. Extension of the ranges of the family Aulostegidae and subfamily Echinosteginae is even greater. The oldest previously known aulostegid, the echinosteginine genus *Limbella* Stehli, first appears in the latest Carboniferous (Virgilian) Gaptank Formation in West Texas.

Archaiosteges harperi, new species
(Fig. 1A–K)

v. 1983 *Pustula* sp., Carter, p. 60.

Holotype.—CM 34953, a large ventral valve from SL 612. Collected by Dr. John A. Harper.

Paratypes.—CM 34954–34958, a small ventral valve and four dorsal valves, all from the same locality as the holotype. All collected by Arthur Gerk of Mason City, Iowa.

Type locality.—SL 612. All of the specimens were collected from one or more of the several coquina beds that occur at various levels within the former west pit (now merged with the former east pit) at the former Hodge's P & M Quarry, Humboldt Co., Iowa (Center Sec. 32, T92N, R28W). This quarry is now owned by the Martin Marietta Corporation and has been greatly expanded. The highly fossiliferous coquinas have all been removed by recent quarrying activities and good fossil collecting is no longer possible (Arthur Gerk, personal communication, December 1990).

Referred material.—Several dorsal valves in the collections of the University of Iowa, Iowa City, also collected by Arthur Gerk from the type locality.

Description.—Ventral valve irregularly subquadrate in outline with straight hingeline; greatest width attained near midlength; visceral disc weakly convex, sloping gently toward margins; trail moderately geniculated, bent nearly normal to plane of visceral disc, and about as long; ears poorly produced, distinguished only by weakly concave flexures; venter slightly flattened but sulcus not developed; ventral interarea moderately short, flattened, strongly apsacline, teeth lacking; elytridium not observed; cicatrix apparently lacking; ornament consisting of numerous irregular rugae which extend onto at least part of trail, and numerous,

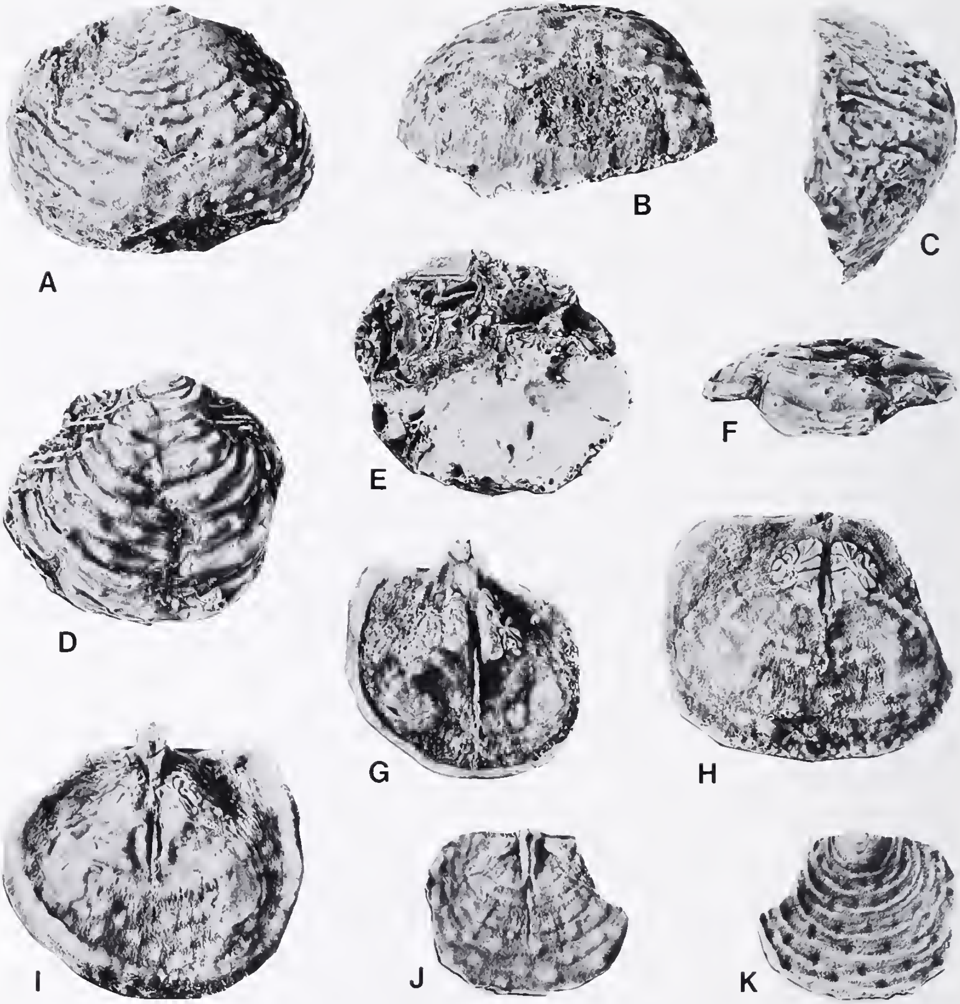

Fig. 1A–K.—*Archaiosteges harperi* n. gen., n. sp. A–C, ventral, anterior and lateral views of the holotype, a large ventral valve, CM 34953, ×2; D–F, ventral, dorsal and anterior views of a small ventral valve paratype, CM 34954, ×3 (note the posterolaterally and laterally directed spines); G–I, three large dorsal valve interiors, paratypes, CM 34955–34957, all ×2; J, K, dorsal and ventral views of a small dorsal valve paratype, CM 34958, ×3.

almost regularly spaced, spine-bearing tubercles; spines of one size, rather fine, directed towards all margins; interior not observed.

Dorsal valve with flattened visceral disc and sharply geniculate short trail; ears weakly delineated by slightly convex flexures; dorsal interarea invariably present, short and anacline, extending full width of hingeline; ornament of rugae and numerous dimples only; spines lacking; interior with large thick cardinal process with quadrilobate myophore and moderately extended shaft in adults; juveniles with erect bilobed cardinal process; lophidium moderately produced; alveolus shallow, accessory muscle scars not observed; median septum obscured by muscle platform posteriorly, appearing as breviseptum anterior to adductor muscle scars and extending forward about two-thirds length of visceral disc; adductor scars moderately raised on low platform; posterior pair strongly dendritic, anterior pair smooth; brachial ridges given off parallel to hingeline just anterior to adductor muscle platform, lobes extending forward almost to marginal rim; lateral ridges parallel to hingeline, merging with distinct marginal rim that surrounds visceral disc; endospines not observed.

Distinguishing characters.—See generic diagnosis above.

Comparisons.—There are no similar Lower Mississippian species described in North America.

Age.—Late Middle or early Upper Tournaisian or Lower Osagian.

ACKNOWLEDGMENTS

This paper was made possible by the generous and much appreciated contributions of specimens by John Harper and Arthur Gerk. Howard Brunton provided valuable advice concerning the morphology and possible relationships of this anachronistic new taxon. Richard E. Grant made useful suggestions for improving the paper.

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